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Notes on Ethological Methods

S. Birger Hansson



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Notes on ethological methods

av

S Birger Hansson

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Rapporten utgör sammanfattning och teoretisk bakgrund till fem artiklar (bilagor till rapporten). Artiklarna illustrerar tillämpligheten hos olika betydelsefulla etologiska forskningsmetoder. Följande metodområden diskuteras: etologiska deprivationsexperiment, etologiska modellexperiment och etologiska observationsstudier. Bakomliggande empirisk forskning har utförts med följande djurarter: Somateria mollissima, Gasterosteus aculeatus och Pterophyllum scalare. Referensram till rapportens metoddiskussion utgörs av en sammanfattning av etologins historia och väsentliga aspekter i etologisk teori och modellbildning.

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NOTES ON ETHOLOGICAL METHODS

by

S. Birger Hansson

The thesis aims at an examination of some important aspects of the methodological problems within ethology. Further, since there exists a mutual relationship between scientific ideas and the methods chosen to test them, the thesis is also concerned with the development of scientific aspects of scientific thought within ethology. The thesis has the following structure:

- I. Theoretical background
 - (1) An attempt at describing ethology and its scientific subject-matter. (I:1-2)
 - (2) A brief account of the development of the scientific ideas of ethology. (I:3-4)
 - (3) The development of scientific ideas in ethology. (I:5-6)
 - (4) The development of scientific ideas in ethology. (I:7-8)
 - (5) The development of scientific ideas in ethology. (I:9-10)
 - (6) The development of scientific ideas in ethology. (I:11-12)
 - (7) The development of scientific ideas in ethology. (I:13-14)
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 - (10) The development of scientific ideas in ethology. (I:19-20)
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 - (14) The development of scientific ideas in ethology. (I:27-28)
 - (15) The development of scientific ideas in ethology. (I:29-30)
 - (16) The development of scientific ideas in ethology. (I:31-32)
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 - (37) The development of scientific ideas in ethology. (I:73-74)
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 - (48) The development of scientific ideas in ethology. (I:95-96)
 - (49) The development of scientific ideas in ethology. (I:97-98)
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The dissertation is based on the following papers:

- Hansson, S.B. (1970). Visual depth discrimination in young eiders (*Somateria mollissima*). Psychol. Res. Bull., Lund Univ., 10, no 13.
- Hansson, S.B., Holmqvist, B. & Strömberg, I.B. (1971). Colour structures and extinction of aggressive display in the male three-spined stickleback (*Gasterosteus aculeatus* L.). Psychol. Res. Bull., Lund Univ., 11, no 11.
- Hansson, S.B. (1973). The influence of stimulus contrast on the aggressive display of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Mimeo. Lund University, Lund.
- Hansson, S.B. (1978a). Notes on the ethological method of observation. I. Selection of behavioural units. Mimeo. Lund University, Lund.
- Hansson, S.B. (1978b). Notes on the ethological method of observation. II. Focal animal sampling. Mimeo. Lund University, Lund.

The thesis aims at an examination of some important aspects of the methodological tradition within ethology. Further, since there exists a mutual relationship between scientific ideas and the methods chosen to test these ideas, the thesis is also concerned with the development of relevant aspects of scientific thought within ethology. Thus the thesis has the following structure:

I. Theoretical background

- (1) An attempt at defining ethology and its specific subject-matter. (I:5)
- (2) A brief account of relevant aspects of the development of scientific thought within ethology. (I:9)

II and III. Empirical studies and methodological considerations.

- (1) The deprivation experiment and its place in ethology:
 - (a) Empirical contribution: Visual depth discrimination in young eiders (*Somateria mollissima*). (II)
 - (b) Concluding discussion. (III:1)
- (2) The model experiment and its place in ethology:
 - (a) Empirical contributions: Colour structures and extinction of aggressive display in the male three-spined stickleback (*Gasterosteus aculeatus* L.), and, The influence of stimulus contrast on the aggressive display of the

male three-spined stickleback (*Gasterosteus aculeatus* L.). (II)

(b) Concluding discussion. (III:6)

(3) Methods of observation and the place of induction in ethology:

(a) Empirical contributions: Notes on the ethological method of observation. I. Selection of behavioural units, and, Notes on the ethological method of observation. II. Focal animal sampling. (II)

(b) Concluding discussion. (III:15)

The rationale behind the choice of these specific methods is that they all bear a clear relation to important theoretical questions. Thus the deprivation experiment is connected with the discussion of the relative impact of learning vs. inheritance on the development of behaviour; the model experiment with the question of identification and relative exclusiveness of activating external stimulation to presumed instinctive actions; the observational techniques with the general ethological bias towards performing inductive work.

A c k n o w l e d g e m e n t s

This thesis is dedicated to my parents.

I want to acknowledge the constructive criticism, support and encouragement of Docent Mats Nyström, Professor Gudmund Smith and Doctor Olof Rydén. I am indebted to my wife Monica Bogren Hansson for her helpful suggestions and comments of the manuscripts.

I. Theoretical background.

E t h o l o g y d e f i n e d

Ethology has been on the move for over forty years. It has become a well-known branch of science, recognized by both biologists and psychologists. Through the popular work of Lorenz, Morris and Ardrey it has even influenced the debate on more general social issues.

In this sense the days of pioneering are over. We have got a fairly good opportunity to grasp the idea of this new science and most psychologists have special thoughts on the topic of ethology. It even happens that we assume a deeper understanding. Thus it is not unusual to hear about the ethological approach, the ethological method and even ethological theory. We have been accustomed to take into account a biological view of behaviour different from that offered by physiological psychology and behaviourism.

This indicates that ethology so far has had a stimulating influence on psychology. But, interestingly enough, it seems to be hard to find any consensus as to what actually constitutes ethology - in other words, what the precise meaning of ethology, or in what respects it differs from e.g. behaviourism, branches of general psychology and physiological psychology. Likewise we may ask in what respects it differs from certain branches of zoology and genetics. Trying to answer these questions we immediately run into difficulties. We have some ideas when speaking of ethology, but these ideas seem unprecise and sometimes even confusing.

Some years ago during the thirties and forties things were all much more simple. Ethology was then connected with one person, namely Konrad Lorenz, and was generally considered as the science of behaviour in his spirit, or for the more initiated in the spirit of those men who met at the first ethological congress. But for those who have become acquainted with the development of the science since then these early conceptions are not wholly relevant.

For one thing, since the early fifties ethology has become more inclusive. Some ethologists of today study not only animal behaviour, as in the pioneering days, they study human behaviour as well, or human behaviour exclusively. Nor can ethology any longer be considered as a science in the spirit of one man or a close group of men. Truly they have put their mark on it, but in this respect too ethology has grown more inclusive. A large number of scientists are today working within the field of ethology and influence its development. Some of these men have even been strongly opposed to the early concepts formulated by the original group.

However, among laymen I think that ethology is still associated with the ideas of Konrad Lorenz and perhaps still thought of as his science. His writings during the sixties and early seventies on social matters have contributed to this view, since they represent that part of ethology which is most easily accessible for the layman. Since some of his writings on these aspects have been highly provocative it should be worthwhile for a moment to consider that any identification of ethology as the science of Konrad Lorenz is misleading. Many of his contributions on theoretical matters are today only of minor interest and have been questioned during the later development of ethology; his writings on human social affairs have either been opposed or left without comment.

Returning to the scope of ethology it was pointed out by Hinde already in 1959 (1959 a) that the ethological approach could not be classified with reference to the kind of phenomena studied. In fact work has been done on animals from the whole animal kingdom ranging from Protozoa to man. Of course during the early days most attention was paid to the behaviour of insects and lower vertebrates, but since then much work has been dedicated to the study of higher mammals, especially non-human primates.

In recent days ethology has thus also contributed to the study of human behaviour, which can be seen as a logical consequence of the interest paid to non-human primates (but certainly also as a necessary consequence of the general Darwinian view of behaviour). Thus ethology has made its contribution to social psychology, developmental psychology and even psychiatry.

In sum when defining ethology there seems to be no reason to restrict the term to the study of infra-human behaviour. The domain of interest covers the whole animal kingdom.

Although the material with which the ethologists are concerned is usually drawn from the behavioural level, the approach is broad and interdisciplinary. Thus different ethological studies could easily be classified into diverse academic disciplines such as physiology, biochemistry, genetics, zoology, taxonomy, psychology, anthropology, sociology and psychiatry.

There has long been a tendency towards reductionism within ethology. It is a common theme in most text-books (e.g. Marler & Hamilton, 1966; Hinde, 1966). In many ethological articles this trend is evident. Choosing a classical study as an example of this the study on cichlid behaviour by Baerends & Baerends-van Roon (1950) is demonstrative. Noticeable in this study are the careful anatomical descriptions which are used as raw material for the behavioural description of movements and displays. Explanations are made in physiological as well as psychological terms. The behavioural description is used as a taxonomic tool. Thus in one and the same article there may be descriptions and explanations on different levels and for different purposes.

This trend towards reductionism which was stressed by Hinde as late as in the meta-discussion in 1959 (1959 a), is today however not unanimous. In some instances the value of such

an approach has been questioned and explanations on a behavioural level recommended (e.g. Baerends, 1975; Dawkins, 1976). With the impact of the new social ethology recent text-books in the same way tend more to stress evolutionary explanations than physiological ones (Alcock, 1975; Brown, 1975).

There is no method unique to ethology (Lorenz, 1958) such as the method of free-associations in psychoanalysis or the method of successive approximations in Skinnerian behaviourism. The method of direct observation is stressed but is not unique to ethology. The new correlational approaches differ in degree but not in quality from those earlier used in psychology. The ecological approach is further not unique. In fact with the exception of a few general papers on these matters by Lorenz (e.g. 1932, 1939) and Tinbergen (e.g. 1948, 1963) methodology was until recently (e.g. Bateson, 1968, Denenberg & Banks, 1968; Slater, 1973; Altmann, 1974 etc.) not much discussed.

The theory of evolution stated by Darwin could be considered as the general paradigm of ethology, but there exists no formal theory or even model to which one could refer when defining ethology (Hinde, 1959 a, Bateson, 1968). During the early fifties two attempts were made in general ethological model-making (Lorenz, 1950; Tinbergen, 1951). As a result of intense discussions within ethology on motivational and developmental topics these were soon markedly reduced in applicability (Hinde, op. cit.; Bateson op. cit.; Blurton Jones, 1972).

There are however two distinguishing characteristics of ethology; one is concerned with the working rationale and the other with attitude.

(1) The unique ethological working rationale was formulated by Tinbergen in his 1963 article on aims and methods of ethology. He argues that the ultimate goal for the ethological inquiry should be to try to reach an answer to four questions which had always been basic to biology, namely those of

causation, function, ontogeny and evolution. Certainly not all these questions are posed in ethological studies, still they constitute a common orientation, a frame of reference which in itself constitutes a distinguishing mark of ethology.

(2) Not entirely separated from the working rationale but more concerned with the men in science than science proper is the question of attitude and emphasis (Hinde, 1959; White, 1974). This attitude could be expressed as a deep interest in the life of wild creatures, an appreciation that the units of behaviour should be natural units evolved by natural selection and that the study of the complexities of nature are valuable objects of research independent of their usefulness in understanding human life (Lehrman, 1971).

The evolution of ethological thought

Early ethology. The impact of Darwin's theory of natural selection on ethology has been tremendous. This impact is based on the Darwinian spirit of empirical determination, its emphasis on naturalistic observations and its refutation of any proposed qualitative gap between man and beast. Even the mixture between phenomenological and behaviouristic language (Christiansen, 1975) evident in Darwin's literature appears in later ethological writings. This influence seems to have been most clear cut in two ways:

- (1) The theory of evolution came to constitute a frame of reference for ethological thinking and observation.
- (2) The comparative method used by Darwin became a forerunner of the comparative analyses later developed within ethology.

The inductive approach emphasized by Darwin became a starting point for ethology. Tinbergen mentions in his 1963 study that the one thing the early ethologists had in common was a wish to return to an inductive start in the behavioural field. Return to observation and description of the enormous variety of animal behaviour and to the simple question: Why do all these animals behave as they do? It should be remembered

that these were the days of early behaviourism, and that the ethologists were reacting against what they rightly considered a wrong and dangerous approach to animal behaviour: i.e. to concentrate on a few phenomena of a few species kept in impoverished environments, and out of such studies to formulate theories which claimed to be universal, and from which hypotheses were deduced and tested. Confronted with early behaviourism the ethologists felt that psychology had skipped the descriptive stage and was soon to lose contact with natural phenomena.

Ethology represented an holistic view of animal behaviour; it became a reaction against behaviourism on one hand, but on the other hand also, like ecology, against certain laboratorial approaches towards animal life within zoology itself (e.g. against comparative anatomy with its interest in mere homology and lack of interest in the questions of function): a reflection of the old controversy between Cuvier and St Hillaire.

The inductive approach is seen from the beginning. In his articles of 1931 and 1932 Lorenz argues that the basic method of ethology should be that of free observation of the natural behaviour of a species. The conduct of (field-) experiments should be secondary (Lorenz, 1935). Already in these early articles the predominant hypothetical variable used in explaining the phenomena observed was that of instinct.

Lorenz's 1935 article is important in many respects. It deals with the key-concept (species specific releasing stimuli for instinct) - concept taken over from von Uexküll - and the role of learning in relation to instinct. Instinct then appears as inherited stereotyped motor patterns unaffected and unaltered by learning during ontogeny. These instincts may however appear together with learned parts of behaviour (intercalations between instinctive acts and conditioned acts) or as an inherited tendency to learn specific aspects of the

milieu(imprinting). Thus we are already in a position to establish a formula for Lorenz's conception of the relation between instinct and learning: development of behaviour: f (inheritence), or f (inheritence + learning), or, f (learning). The formula is important since (with the exception of the conception f (learning) which later on was abandoned) Lorenz would never change it, and it was to give rise to a great controversy during the fifties and sixties.

The argumentation in Lorenz's Rostock lecture (1939) is that inherited stereotyped motor patterns differ qualitatively from other behaviour. The point is that instinctive acts show such a constancy that they could be treated like morphological characters. Related groups of animals could then be shown to possess homological motor patterns; instinctive acts could be pursued through phylogeny. Behaviour could become a taxonomic tool (a critical treatment of the concept of homology is presented by e.g. Atz, 1970).

The cooperation between Lorenz and Tinbergen began with the study on egg-rolling in the grey-lag goose(1938).Tinbergen had however made several contributions to the naturalistic study of animal behaviour and Dutch ethology was well getting into the stride before Lorenz became well known (Baerends, Beer & Manning, 1975). Yet with the publication of Lorenz's 1935 article Tinbergen began interpreting his observations in Lorenzian terms. The most outstanding papers during these early days by Tinbergen are the short paper on the behaviour of sticklebacks made with ter Pelwijk (1937) and the study on the gaping responses of young black birds and thrushes (Tinbergen & Kuenen, 1939).

These early studies are important since Tinbergen in introducing the model experiment (a technique which was already known) in these instances indicates the usefulness of controlled experimentation in ethology. Thus almost from the beginning experimentation was used alongside of observation. The model

experiment should be important in the identification of key stimuli, i.e. species specific external activating forces. Work with these experiments culminated with Tinbergen's article in 1948 on social releasers. During the seventies the technique has in some instances been questioned (Wootton, 1971; Brown, 1975).

The energy-models of motivation

In 1950 Lorenz's model of motivation was completed and in 1951 Tinbergen presented The study of instinct. The central contribution in Lorenz article is the refinement of the motivational concepts already sketched in 1937. By an analogy with an hydraulic machine Lorenz suggested that action specific energy is produced by specific structures in the central nervous system. When a certain amount of this action specific energy has been accumulated the organism is considered to possess an internal motivation for a specific action. The discharge of energy is dependent on two causal factors: (1) the level of action specific energy attained, and, (2) the amount and effectiveness of external stimulation. The discharge may be caused by internal factors alone, by strong external stimulation alongside of moderate internal stimulation or the reverse.

Tinbergen made several important modifications of the Lorenzian model. Instead of postulating motivational energy the action specificity of which was restricted to a specific, limited response pattern, Tinbergen suggested that motivational energy was general to all activities of a major instinct. Thus he replaced Lorenz's concept of action specific energy with what might be called drive-specific energy - the same type of energy could activate all the diverse sensory-motor mechanisms under e.g. the reproductive instinct. (It should be remembered that Tinbergen, 1951, e.g. in Chapter V is not consequent in using either "instinct" or "drive").

Lorenz had suggested a hierarchy of moods in his model (mood:

readiness for action). This hierarchical concept was elaborated by Tinbergen into a hierarchical model of instincts (cf. 1951, p. 110-111). Tinbergen suggested energy general to a major class of instincts. Sub- (part) instincts within this class and on different levels were suggested to be motivated by energy specific to them (from a superior motivational center and from the center on the specific level). Thus he assumed the existence of a sequence of instincts each leading to a sub-goal and in the end to the final instinctive (con-summatory) act.

The highest level in this hierarchy constituted endocrine responses to a general class of stimulation. Regarding the intermediate and lower levels however the outflow of energy from respective motivational centers had to be released by specific reflex-like mechanisms called Innate Releasing Mechanisms (IRM) acted upon by specific external stimulation. The demand on specificity in this respect was said to increase with the progressive flow of energy down the hierarchy.

The hierarchical sequentiation of sub-instincts within a major instinct was further suggested to correspond with similar hierarchical organisation of the nervous system.

The manner in which a specific sub-instinct appeared was formulated in the following way. Sign stimulus (key stimulus)
 --- IRM --- FAP (Fixed action pattern).

Thus behaviour was explained in a reductive manner. An outstanding example of this reductive trend can be seen in the explanations offered for the displacement phenomenon. Displacement means in ethology the appearance of a seemingly irrelevant behaviour within a behaviour chain. It was observed that such behaviours occurred when the proper outlet of energy was blocked. The phenomenon was then explained by reference to energy flowing over from the blocked center to an adjacent one, thereby causing the occurrence of an irrelevant action.

The controversy; modern ethology.

The work during the pioneering period had been dominated by and centered around a small group of enthusiasts. In the early fifties ethology, however, slowly began to attract the interest of others working outside this small group. This was not exceptional, the ethologists had formulated elegant (and simple) models of animal behaviour, and with their biological frame of reference they promised a modern synthesis of behaviour. Further some of the new ideas had been rather provocatively presented. Beer (1975) points out that this new attraction came to have two consequences:

(1) People outside the original group adopted the viewpoints and the ideas and attached themselves more or less to the original group. Thereby the small and closely knit group broadened. (2) Voices were raised in protest to and in criticism of the claims of the group on matters of method, theory and interpretation.

As a result of this criticism, the accumulation of new data, influence from branches outside ethology and as a result of this new flow of people over to ethology, the original group lost some of its influence. Thus during the fifties and sixties many factors interacted in breaking up an earlier homogeneity. Ethology ceased to be an easily identified science and ceased to be a pioneering science.

Lehrman presented in 1953 a critical paper mainly centered around the issue of development which came to have great influence on ethology. Lehrman represented the American science of animal behaviour originated around the curator of the Natural Museum in New York T.C. Schneirla. Schneirla was a naturalist (he was not, as has been suggested, a member of the behaviouristic school - he was in fact against it) but was opposed to many of the pet concepts of early ethology (such as instinct - which he considered to be unscientific).

One of Schneirla's fundamental conceptions was a rejection of

any supposed dichotomy between unlearned (instinctive) and learned behaviour. Already in 1935 he argues that at a given phyletic level and at a given ontogenetic stage the total behaviour of an individual will be determined by the prior and continuous interaction and fusing of growth and maturational processes with the genome, as a derivate of the individual's continuous experience. At higher levels of phylogeny and at higher levels of ontogeny specific learning processes should be involved in the maturational process (Maier & Schneirla, 1935).

It should be noted that for Schneirla learning was not to be considered as a unitary process but was something which occurred at different levels of complexity. Dealing with animal behaviour the use of the term learning should in many cases further be considered as synonymous with what otherwise is called experience.

Thus in contrast to the formula presented in connection with the discussion of Lorenz's 1935 paper the general formula of behavioural development favoured by Schneirla could be formulated in the following way: f (inheritance $\times$ experience).

In line with this, Lehrman's critique was directed against that earlier proposed dichotomy between inherited and acquired behaviour. The critique centered around two points: (1) in many cases the ethological proposal on inherited determinants had been made in absence of facts, and (2) a proposed dichotomy hinders a proper study of the developmental processes which seeks to get such facts.

Lehrman further criticized the proposed motivational mechanisms claiming that they were based on preconceptions and loose analogies rather than on empirical facts. In the same way he criticized the apparent element of anthropomorphism in ethological thinking. This is important since the already apparent tendency towards phenomenological interpretations of

data coexisting with behavioural interpretations evident in Lorenz's early writing would later reappear in the form of uncovered animorphism in his book on aggression (1963).

The 1953 paper started an intense discussion within ethology which lasted for several years until at the end of the fifties, it seemed to have faded (Beer, 1975). Actually, the paper seems to have become a dividing point between Lorenzian ethology and Anglo-Saxon ethology with reference to the extent to which the ideas and the criticism were assimilated. This conclusion might be drawn when reading the 1961 book on evolution and modification of behaviour where Lorenz distinguishes between Anglo-Saxon ethologists and himself on the basis of their respective treatment of the nature-nurture problem.

The discussion led to reformulations in many ways. Most conspicuous during these years were the articles on the concept of unitary drives and energy models (Hinde, 1959 b, 1960) where the concept of motivation was scrutinized. Further we find the new interpretations of the displacement concept (reviewed by Ziegler, 1964) where the conflict model was questioned, and finally the discussion on the utility of the concept of sign stimulus (Marler, 1961).

Thus there was a gradual assimilation of new ideas and towards the end of the fifties it seemed as though the dichotomy between innate and acquired behaviour and the proposed conceptualisation of motivation had been given up.

In 1961 Lorenz's book Evolution and Modification of Behaviour was published in German. Sadly enough the appearance of this book meant that the old dichotomy between innate and acquired behaviour was once again brought out. The old conceptualisation was now stated in another way, but some of the formulations were still disputable. These were the ideas put forward by Lorenz:

(1) He recognizes the importance of experience in the process

of development, but the process of acquisition is in itself determined by the genome. This possesses a blueprint in accordance with which behaviour will develop and the organism assimilates from the external world what is in accordance with this blueprint. Thus the genome makes us selective learners.

(2) There exist behaviours which are strictly determined, behaviours which develop only when given necessary sensory stimulation. Such a behaviour is innate and the existence of such innate behaviour patterns can be proved by the deprivation experiment (i.e. the organism is reared under conditions which exclude information necessary should the behaviour develop through learning). The organism may be extremely selective as to what it will learn, to offer alternative information to see if a certain behaviour pattern will develop differently may in that case be of no use.

In conclusion the modified model offered by Lorenz is still an additive model, and very similar to the earlier conception of imprinting.

In 1966 the first edition of Hinde's book Animal behaviour a synthesis of ethology and comparative psychology appeared, in which the new Lorenzian model is questioned. Likewise Tinbergen, in his 1963 article, spoke a softer language. In general the rebirth of the controversy did not seem to have altered much in the new development of ethology. The discussion was finally brought to an end with Lehrman's article in 1970. In this paper Lehrman stressed the fact that there seemed to have been a confusion brought about by the terminology chosen. The term innate had been used to denote both inherited and autonomously developed behaviour. Lehrman stated that the study of heritability requires the use of breeding experiments by which the distribution of the trait in a population can be compared to the distribution of genetic affinities. Whether a behavioural trait is autonomously developed is quite another question. The experiments needed

for this kind of study are not genetic experiments but developmental studies, i.e. studies on the development of the trait in individuals. These should not be interpreted in genetic terms; they should be interpreted in developmental terms.

Lorenz's 1961 book is written in a strikingly emotional tone. There could be two reasons for this. On one hand the difference in viewpoint may reflect differences in tradition between American and European ethologists (as suggested by Lehrman, 1970 and Beer, 1975). On the other hand without the concept of innateness ethology could lose some of its identity, become less a specific branch of zoology and drift away.

It may be more than a coincidence that during these years Lorenz started to develop ethology into a more general behavioural science. The cornerstone in his writings on human social matters was the concept of instinct. Without a less certain scientific ground for this concept his writings in social psychology should become meaningless.

With the exception of some contributions to the Montagu-book (1968) Lorenz's philosophical issues were however not commented on much by ethologists.

The further development of ethology implied that all ideas of making grand theories were given up. Explanations became more limited in scope and in the process they have converged with those offered by psychologists (Bateson, 1968). Prominent features in this new development have been studies on feedback and processes of attention (e.g. McFarland, 1971; Andrew, 1976).

In the late sixties a new branch of ethology was established, namely that of social ethology. Thus interest turned from a preoccupation with the single animal or the dyad to interest in group-processes. The departure of this new branch from

classical ethology could be dated to 1970 when the programme declaration by Crook appeared. In this he argues that ethology had paid too much attention to dyadic behaviour and treated social behaviour in terms of reciprocal interaction between individuals presenting stereotyped signals to each other, signals which were commonly suggested to be species specific and considered as little affected by learning. Crook concludes that this could constitute a basis for the analysis of societies given that societies were programmed entirely in this way. Unfortunately they are not. It is a failure of classical ethology not to consider social behaviour in terms of group processes.

According to Crook, ethology should study the relations between individuals and the natural group, considered as the social environment within which individuals live and to which they are adapted. Social ethology should be interested in social behaviour, population dynamics and ecology. As a matter of fact an effective ethology should be based primarily on social considerations.

It is significant that most proponents of this new approach to behaviour work with mammals and especially primates, in contrast to the early ethologists who preferred to work with the lower vertebrates. The new discipline considers itself to be an eclectic discipline open for information from relevant branches of science, although it is evident that what social ethology will contribute is the Darwinian view of behaviour. The influence of social learning is stressed (Crook, 1970 b) and role concepts (i.a. Gartlan, 1968) are used.

The last branch on the ethological tree is that of "sociobiology". The birth of this school could be dated to 1975 when Wilson's book Sociobiology appeared. The term sociobiology had before that been used many times and these earlier works should not be confused with the school of

socio-biology.

According to Wilson socio-biology is the systematic study of the biological basis of all social behaviour. His book makes an attempt to codify socio-biology into a branch of evolutionary biology and particularly of modern population biology.

In Wilson's book, socio-biology is an entirely zoological affair much as Lorenz's ethology was. One of his adherents (Barash, 1977) has however recently also invited interested scientists from other camps to join the family; social psychologists especially are assumed to be interested.

The kind of explanations offered in Wilson's book rest heavily on the evolutionary theory. The instinct concept is retained and especially the view of the genome as containing a blueprint making people and animals selective learners is stressed (the instinct concept is modernized in Barash's book; probably the two books are intended for different readers).

The pet theory of socio-biology is that of kinship selection (Hamilton, 1964). This states, that individuals may offer themselves, i.e. sacrifice their own reproductive output, in favour of helping genetically related individuals to reproduce. This may lead to a propagation of one's own genes (carried by the relatives) more efficiently than selfish attempts to maximize productions on one's own offspring.

With this theory as a supplement to the Darwinian theory Wilson (and Barash) are able to explain quite complex human affairs, such as religion and ethics. By considering evolution as a running process always and continuously working and influencing the organism through the blueprint in the genome they can in fact explain practically everything which has to do with social behaviour. "Scientists and humanists

should consider together the possibility that the time has come for ethics to be removed temporarily from the hands of the philosophers and be biologized" (Wilson).

Thus again the ontogenetic development is seen as an additive process (gene action + individual experience) not as an interactive process.

Barash suggests that socio-biology with its emphasis on evolution may provide a general paradigm for human social psychology. This may be. However, it seems hard to conduct empirical research based on the recommendations made by Barash and Wilson, since they are mostly concerned with ultimate explanations. Before considering socio-biology as a suitable general paradigm we must ask how to prove these ultimate explanations, and further what they can offer to understanding of the individual (human) behaviour, in groups or otherwise.

The reductionistic trend is most evident when Wilson discusses human behaviour. In a discussion on sociology he asserts that the transition from purely phenomenological theory must await a full neurological explanation of the brain, the same goes for psychological matters like stress, learning and cognition.

The new socio-biology is assumed to be a universal theory of behavioural biology. Ethology and comparative psychology will soon (in the year 2 000) be cannibalized by neuro-physiology and sensory physiology from one end and by behavioural ecology (socio-biology) from the other. Wilson hopes that those scientists concerned will not be offended by his prophecy.

However, such declarations should not conceal the fact that there are sensible approaches to human behaviour within ethology offered by scientist such as Hinde, Tinbergen and

Blurton Jones. It must obviously be realised with caution and consideration that although man is a creature he is a very complex creature. The main contribution of modern ethology to human psychology seems to be:

- (1) An emphasis on comparative studies (e.g. Hinde's studies on mother/infant relations in *Rhesus* monkeys, e.g. 1974).
- (2) An emphasis on direct observation as a powerful tool not only for description but also for causal analysis, especially in developmental psychology (e.g. Blurton Jones, 1972; McGrew, 1972) but also in the study of psychiatric disorders (e.g. Grant, 1968; Tinbergen, 1972; c.f. also Hutt & Hutt, 1970; White, 1974; McGuire & Fairbanks, 1977).

The assumptions behind the new human ethology are twofold:

- (1) To give the traditionally "soft" sciences of child development and social behaviour a useful opportunity to make themselves a little "harder" without at the same time getting as narrow-minded as might result from too successful an imitation of the physical sciences (Blurton Jones, 1972).

- (2) By gradually building up an ethogram of our species, ethology could provide the yardstick by which behavioural pathology can be measured (Tinbergen, 1972; cf. Grant, 1969; McGrew, 1972).

The ethologist's emphasis on observation and causal analysis constitutes a valuable addition to the established approaches in some fields of psychology. However, it should also be brought out clearly that the naturalist's conviction that the "hard way" is the better way is wrong. In some instances the "hard way" might be the right way, in others it is certainly not.

The second argument (ethogram building) sounds striking enough but it is questionable if it really is worth the enormous work which must be laid down. For one thing psychiatrists already have a lot of information as to what constitutes normal

behaviour according to some definition and what constitutes deviant behaviour. Secondly the enormous individual variations characterizing the human species makes Tinbergen's strategy worthwhile only in specific cases.

Human ethology with the exception of socio-biology is the last established branch of ethology. It is a new science and the time has not yet come to judge its influence on psychology.

It may be that the most valuable contribution that human ethology and general ethology will make to psychology is a pronounced emphasis on the view of man as a biological organism, as another member of the animal kingdom. Such a pronounced emphasis might counteract prevalent tendencies within psychology to make it a purely humanistic endeavour.

R e f e r e n c e s

- Alcock, J. (1975). Animal behavior: An evolutionary approach. Sunderland: Sinauer Associates.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49, 227-267.
- Andrew, R.J. (1976). Attentional processes and animal behaviour. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge: Cambridge Univ. Press.
- Atz, J.W. (1970). The application of the idea of homology to behavior. In L.R. Aronson, E. Tobach, D.S. Lehrman & J.S. Rosenblatt (Eds), Development and evolution of behavior. Essays in memory of T.C. Schneirla. San Francisco: Freeman.
- Baerends, G.P. & Baerends-van Roon, J.M. (1950). An introduction to the study of the ethology of cichlid fishes. Behaviour, suppl. 1.
- Baerends, G.P. (1975). An evaluation of the conflict hypothesis as an explanatory principle for the evolution of displays. In G. Baerends, C. Beer & A. Manning (Eds), Function and evolution in behaviour: Essays in honour of professor Niko Tinbergen. Oxford: Clarendon Press.

- Baerends, G.P., Beer, C. & Manning, A. (1975). Function and evolution in behaviour: Essays in honour of professor Niko Tinbergen. Oxford: Clarendon Press.
- Barash, D.P. (1977). Sociobiology and behavior. New York: Elsevier.
- Bateson, P.P.G. (1968). Ethological methods of observing behavior. In L. Weiskrantz (Ed.), Analysis of behavioral change. New York: Harper & Row.
- Beer, C.G. (1975). Was professor Lehrman an ethologist? Anim. Behav., 23, 957-964.
- Blurton Jones, N. (1972). Characteristics of ethological studies of human behaviour. In N. Blurton Jones (Ed.), Ethological studies of child behaviour. Cambridge: Cambridge Univ. Press.
- Brown, J.L. (1975). The evolution of behavior. New York: Norton & Co.
- Christiansen, J.T. (1975). Darwin, Lorenz, Reventlow et videnskabs-teoretisk studium. In K.B. Madsen (Ed.), Psykologi og videnskabssteori. København: Munksgaard.
- Crook, J.H. (1970 a). Social organization and the environment: Aspects of contemporary social ethology. Anim. Behav., 18, 197-209.
- Crook, J.H. (1970 b). The socio-ecology of primates. In J.H. Crook (Ed.), Social behaviour in birds and mammals. London: Academic Press.
- Darwin, C. (1859). On the origin of species. London: Murray.
- Darwin, C. (1872). The expression of the emotions in man and animals. London: Murray.
- Dawkins, R. (1976). Hierarchical organisation: a candidate principle for ethology. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge: Cambridge Univ. Press.
- Denenberg, V.H. & Banks, E.M. (1962). Techniques of measurement and evaluation. In Hafez, E.S.E. (Ed.), The behaviour of domestic animals. London: Balliere, Tindall & Cox.
- Gartlan, J.S. (1968). Structure and function in primate society. Folia Primatologica, 8, 89-120.
- Grant, E.C. (1968). An ethological description of non-verbal behaviour during interviews. Br. J. Med Psychol., 41, 177-184.

- Grant, E.C. (1969). Human facial expression. Man, 4, 525-536.
- Hamilton, W.D. (1964). The genetical theory of social behaviour: I and II. J. Theoretical Biol., 7, 1-52.
- Hinde, R.A. (1959 a). Some recent trends in ethology. In S. Koch (Ed.), Psychology: a study of science, Vol. 2. New York: McGraw-Hill.
- Hinde, R.A. (1959 b). Unitary drives. Anim. Behav., 7, 130-141.
- Hinde, R.A. (1960). Energy models of motivation. Symp. Soc. exp. Biol., 14, 199-213.
- Hinde, R.A. (1966). Animal behaviour: A synthesis of ethology and comparative psychology. London: McGraw-Hill. Second edition: 1970.
- Hinde, R.A. (1974). Mother/infant relations in rhesus monkeys. In N.F. White (Ed.), Ethology and psychiatry. Toronto: Univ. Toronto Press.
- Hutt, S.J. & Hutt, C. (1970). Direct observations and measurement of behavior. Springfield: C.C. Thomas.
- Lehrman, D.S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. Quart. Rev. Biol., 28, 337-363.
- Lehrman, D.S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L.R. Aronson, E. Tobach, D.S. Lehrman & J.S. Rosenblatt (Eds), Development and evolution of behavior: Essays in memory of T.C. Schneirla. San Francisco: Freedman.
- Lehrman, D.S. (1971). Behavioral science, engineering and poetry. In E. Tobach & L.R. Aronson (Eds), The biopsychology of development. New York: Academic Press.
- Lorenz, K. (1931). Beiträge zur Ethologie sozialer Corviden. J. Ornithol., 79, 67-127.*
- Lorenz, K. (1932). Betrachtungen über das Erkennen der art-eigenen Triebhandlungen der Vögel. J. Ornithol., 80, 50-98.*
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. J. Ornithol., 83, 137-213, 289-413.*

* English version in: Studies in animal and human behaviour. Vol. 1, London: Methuen (1971).

- Lorenz, K. (1937). Über die Bildung des Instinktsbegriffs. Die Naturwissenschaften, 25, 289-300, 307-318, 324-331.*
- Lorenz, K. (1939). Vergleichende Verhaltensforschung. Verhandlungen der Deutschen Zoologischen Gesellschaft, Rostock. Zoologischer Anzeiger, Suppl., 12, 69-102.
- Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. Symp. soc. Exp. Biol., 4, 221-268.
- Lorenz, K. (1958). Methods of approach to the problems of behaviour. The Harvey Lectures 1958-1959. New York: Academic Press.**
- Lorenz, K. (1965). Evolution and modification of behavior. Chicago: Univ. Chic. Press (German version 1961).
- Lorenz, K. (1966). On aggression. New York: Harcourt Brace Jovanovich (German version 1963).
- Lorenz, K. & Tinbergen, N. (1938). Taxis und Instinkthandlungen in der Eirollbewegung der Graugans I. Z. Tierpsychol., 2, 1-29.
- Lorenz, K. & Leyhausen, P. (1973). Motivation of human and animal behavior: An ethological view. New York: van Nostrand Reinold.
- Maier, N.R.F. & Schneirla, T.C. (1935). Principles of animal psychology. London: McGraw-Hill.
- Marler, P. (1961). The filtering of external stimuli during instinctive behaviour. In W.H. Thorpe & D.L. Zangwill (Eds), Current problems in animal behaviour. Cambridge: Cambridge Univ. Press.
- Marler, P. & Hamilton, W.J. (1966). Mechanisms of animal behavior. New York: J. Wiley.
- McFarland, D.J. (1971). Feedback mechanisms in animal behaviour. London: Academic Press.
- McGrew, W.C. (1972). An ethological study of children's behavior. London: Academic Press.
- McGuire, M.T. & Fairbanks, L.A. (1977). Ethological psychiatry: psychopathology in the context of evolutionary biology. New York: Grune & Stratton.

* English version in: Studies in animal and human behaviour. Vol. 1, London: Methuen (1971).

** English version in: Studies in animal and human behaviour. Vol. 2, London: Methuen (1971).

- Montagu, M.F.A. (Ed.). (1968). Man and aggression. Oxford: Oxford Univ. Press.
- Pelwijk, J.J. ter & Tinbergen, N. (1937). Eine Reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. Zeitschr. Tier-Psychol., 1, 193-201.
- Slater, P.B.J. (1973). Describing sequences of behavior. In P.P.G. Bateson & P.H. Klopfer (Eds), Perspectives in ethology. New York: Plenum Press.
- Tinbergen, N. (1948). Social releasers and the experimental method required for their study. Wilson Bull., 60, 6-52.
- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press (new ed. 1969).
- Tinbergen, N. (1963). On aims and methods of ethology. Zeitschr. Tierpsychol., 20, 410-433.
- Tinbergen, N. (1971). Foreword in N. Blurton Jones (Ed.), Ethological studies of child behaviour. Cambridge: Cambridge Univ. Press.
- Tinbergen, N. (1972). Early childhood autism - an ethological approach. Advances in ethology, 10, 1-53.
- Tinbergen, N. & Kuenen, D.J. (1939). Über die auslösenden und die Richtunggebenden Reizsituationen der Sperrbewegung von jungen Drosseln (*Turdus m. merula*, L. und *T.e. ericetorum*, Turton), Zeitschr. Tierpsychol., 3, 37-60.
- White, N.F. (Ed.). (1974). Ethology and psychiatry. Toronto: Univ. Toronto Press.
- Wilson, E.O. (1975). Socio biology: The new synthesis. Cambridge: Harvard Univ. Press.
- Wootton, R.J. (1971). Measures of the aggression of parental male three-spined sticklebacks. Behaviour, 40, 228-262.
- Ziegler, H.P. (1964). Displacement activity and motivational theory. A case study in the history of ethology. Psychol. Bull., 61, 362-376.

II. Empirical studies.

PSYCHOLOGICAL RESEARCH BULLETIN

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*Visual Depth Discrimination in Young Eiders
(Somateria mollissima)*

by S. Birger Hansson



LUND UNIVERSITY SWEDEN

A b s t r a c t. Visual depth discrimination in young eiders was investigated by means of a "visual cliff". The sample was divided into two groups, both of which had been visually deprived from birth, one group then being given a period of exposure on either the shallow or the deep side before testing. In the testsituation all the completely naive subjects preferred the shallow side, while those in the other group tended to choose in accordance with the type of exposure given.

P r o b l e m

Shortly after hatching, eider chicks follow the female into the water. In so doing they pass a visual cliff, i.e. they cross over from land to water. This crossing over is then repeated continually during later life. At the same time, experiments show that higher organisms tend to avoid depth (Thorndike, 1899; Russel, 1932; Lashley & Russel, 1934; Kurke, 1954; Walk, Gibson & Tighe, 1957; Gibson & Walk, 1960; Walk & Gibson, 1961; Emlen, 1964), provided they are aware of and cannot overcome it. Does the behavior of eider chicks depend then on the fact that they fail to discriminate depth so early in life? Or is the crossing-over a consequence of the imprinting to the female? These questions became starting-points for our work. Only the first will be dealt with in this study. The latter question will be examined in connection with coming field-studies.

The area of investigation as a whole relates to two postulates in the theories of Lorenz and Tinbergen concerning innate releasing-mechanisms (AAM and IRM respectively) and fixed motor pattern (FMP), namely:

- (1) A fixed motor pattern will develop as a response to a sign-stimulus without earlier learning.
- (2) This connection is then little affected by later learning. (Lorenz, 1935; Tinbergen, 1951).

In our situation it is possible to compare to a certain degree both the visual cliff with the sign-stimulus and the choice-behavior with the motor pattern. Certain operational definitions are involved in the questions considered:

(1) Is the ability of eider chicks to discriminate depth inborn or is it acquired through early learning? Here we define the ability to discriminate depth as the tendency to avoid the deep side in favour to the shallow when faced with a choice between the two.

(2) Is it possible by exposing visually naive eider chicks to a deep or to a shallow side alone to make them in a choice-situation later choose that side which they have experienced?

A p p a r a t u s

As indicated already, the experiments required use of a "visual cliff apparatus" (Walk & Gibson, 1961).

Main apparatus. Two horizontal planes were arranged at different heights with a discrete crossing so that a cliff appeared. The difference in height was 50 cm. A grey-painted vertical septum became the wall of the cliff. Patterns of black points randomly distributed on a white background were evident upon the two plains. Each point was 4 mm in size. The proportion of black to white was 1:1. The pattern on each plane was covered with a plexiglass disk 3 mm in thickness. This visual cliff was placed in a cylinder of semi-transparent plastic measuring 100 x 50 cm.

For the test a fine wire-mesh screen fastened between two metal sticks was used as bridge. The dimensions of the bridge were 6 x 50 cm and the size of the mesh 1 cm². The bridge ran longitudinally from one side of the cylinder to the other. It was fixed at a height of 6 cm above the pattern by means of transparent nylon wires hanging from the upper edge of the cylinder.

In order to isolate the visual cliff from sound, a box of square porous paper plates 100 x 50 cm in size was built around the cylinder. Two lamps were hung in each of the four corners of the box at heights of 25 and 75 cm respectively; the intensity of the light was set at about 100 lux during testing and exposure. A square plate 80 x 80 cm was used as a cover; its underside was painted black and was covered with gauze to prevent visual impressions from being obtained on the inside, since two observation holes were located 2 cm from the outer edge of the plate opposite from one another.

For the exposures no bridge was used but rather an upright vertical septum of paper which divided the cylinder into one chamber with a deep pattern and one with shallow. In addition, two simplified visual cliffs square in form were employed as an exposure apparatus in some cases.

E x p e r i m e n t a l a n i m a l s

52 specimens of *Somateria mollissima* (Anatidae) which had been collected on various occasions from different litters during the hatching-season May-June functioned as experimental subjects.

The sensory equipment of eider chicks, as of birds in general, is comparatively good (Pumphrey, 1948). Their locomotive power develops rapidly: they shuffle after 5-6 hours and perform walking movements relatively well after approximately 12 hours (Fabricius, 1951). The chicks are calm and easy to handle.

P r o c e d u r e

Handling of the animals. The eggs were hatched in a darkened hatcher in which relative humidity was 75% and temperature 38°. Control for newborn chicks was made every fourth hour. The time of birth was calculated as the mean between the time of the preceeding control and the of current one. The newborn chick was placed in a darkened plastic box which was then placed in another hatcher, darkened also. During transport to and from the laboratory the plastic boxes were kept in a bag lined with foam plastic (light- and sound isolating).

Procedure of exposure (1) and testing (2). The animals were transferred from their boxes to the apparatus in darkness.

(1) The animal was placed in the right-hand chamber; the light was switched on and exposure began. Occasionally it was necessary to interrupt this procedure for cleaning. The animal was then transferred to its box to wait - all of this in darkness.

(2) At testing the animal was placed on the bridge and the light was then switched on. Testing was conducted individually and without the observers knowing to which group the animal belonged. At the end of each ten-minute period the light was switched off and the animal was turned 180° on the bridge relative to the starting-point. As a rule, the whole procedure was finished after the end of the period in which a choice had been made (choice: to jump down). The animal was observed continuously during testing, behavioral manifestations and their time of occurrence being noted.

D e s i g n

On the basis of the problems posed, the study was divided into two sub-parts: choices with naive subjects, and with those previously exposed.

Naive choices: Seven subjects spread along the age-continuum und without any visual experience were used.

Choice-trials with subjects which had been exposed: The experimental groups consisted of 41 subjects in all. Of these 20 were given exposure on the shallow side and 21 on the deep. In addition, four time-variables were manipulated in the experimental group: (1) The age of the subjects at the beginning of the exposure and (2) the age at testing, (3) the interval between exposure and testing, and (4) the length of exposure.

For control purposes we endeavored to match the subjects for the two exposure conditions in pairs such that in relevant aspects they were as alike as possible.

R e s u l t s

The results can be divided into three categories: the actual choice-results, the latency-times of choices, and various other behaviorial manifestations (oscillation between sides after choice, frequency of pluming behavior, frequency of looking behavior prior to choice, and frequency of pecking behavior). Since the groups are small, strong tendencies will be noted, even if not significant. The following notations are employed in the analysis: C-control-

group, Se- shallow-exposed subjects, De- deep-exposed subjects, Sc- shallow-choice and Dc- deep-choice.

Naive choices. All subjects without visual experience preferred the shallow side to the deep.

Choice-trials with subjects which had been exposed:

Prior exposure produced differences in choice between the groups De/Se and De/C. It was found that De preferred the deep side more than did the other groups (see Tables I and II).

Time-variables: Age of more than 55 hours at the beginning of testing, as well as exposure of more than 24 hours, yields significant differences in that $De > Se$ and $De > C$ (see Table II).

Both a 0-interval and an interval of more than 24 hours produce significant differences ($De > C$ under both conditions, $De > Se$, but only significantly so for an interval of more than 24 hours).

Age at exposure gives contradictory results. This variable seems unimportant.

Latency-times: Group comparisons of latency times $DeDc > DeSc$ and $SeSc > DeSc$ reveal significant mean differences and $DeDc > SeDc$ a weak tendency of the same type (see Table III).

De: deep-exposure; Se: shallow-exposure;
Dc: deep-choice; Sc: shallow-choice.

Other behavioral manifestations: For three variables, statistically significant differences can be shown: for the pluming-variable, the oscillation-variable and the looking-variable. In addition, for the pecking-variable non-significant tendencies are evident (see Table III).

As regards the pluming-variable significant differences are found in the comparisons $De < Se$ and $DeDc < SeDc$, and trends in $DeDc < DeSc$ and $DeDc < SeSc$.

The oscillation variable differs significantly in the comparisons $SeDc > SeSc$ and $DeSc > SeSc$. Also tendencies can be noted in the comparisons $Se < De$, $DeDc > SeSc$ as well as $Wrong-c > Right-c$.

The looking variable yields a significant difference in the final period ($DeDc > SeSc$) and a tendency of the same sort for the directions of looking during that period.

Table I. Choice-trials, the groups C/Se/De (the entire material) and the groups Se/De.

Choice	G r o u p		
	C	Se	De
Sc	7	17	12
Dc	0	3	9

$X^2_{total} = 6.97$; $P = .05$ (Df=2); one-tailed. Fisher $_{Se/De} : P = .03$, one-tailed.

Table II. Choice-trials, all significant differences and trends.

Group	Variables				Total
	Age at exposure (hrs)	Age at testing (hrs)	Length of exposure (hrs)	Length of interval (hrs)	
	$\begin{matrix} < 24 \\ 24 - 48 \\ > 48 \\ < 30 \\ > 30 \end{matrix}$	$\begin{matrix} < 55 \\ > 55 \end{matrix}$	$\begin{matrix} < 12 \\ 12 \\ 24 \\ < 12 + 12 \end{matrix}$	$\begin{matrix} 0 \\ 1 - 24 \\ > 24 \\ 1 - 24 + > 24 \end{matrix}$	
Se/De/C	-----				.03
Se<De	.14 .20 .05	.07	.03	.08 .05	.03
Se<C					
De>C	.05 .11 .04	.13 .02	.01	.04 .02	.04

De: deep-exposure; Se: shallow-exposure;
 Dc: deep-choice; Sc: shallow-choice.

Table III. Other behavioral manifestations and latency-times compared within different exposure and choice groups, (all significant differences and marked trends are shown).

V a r i a b l e s

Group	Pecking			Vocalisation	Looking		Latency-times
	The entire period	The initial 10 min.s.	The final 10 min.s.		The entire period	The final 10 min.s.	
				Pluming - the entire period			
				Oscillation - the entire period			
				The entire period			
				The initial 10 min.s.			
				The final 10 min.s.			
De/Se	.20			.05			
DeDc/SeSc				.01		.04	
DeDc/DeSc		.15		.08			.05
DeDc/SeDc	.16			.13			.10
DeSc/ScDc		.12					
SeSc/SeDc				.05			.001
SeSc/DeSc				.03			
Right-/							
Wrong-c							
(1 or 0)		.13		.10			

Legend: Pecking: bill movements against bridge or wall;
 Pluming: bill movements in the plumage;
 Oscillation: moving between deep or shallow side;
 ← indicates direction of significances (i.e. De/Se
 0.20: De<Se).

D i s c u s s i o n

Naive choices: Our results with complete visual deprivation prior to testing appear to complement the observations of Walk & Gibson (1961), since with the species investigated here too the ability to discriminate depth seems to be given from the start. However, the subjects may well have learned to discriminate depth during the short time while in the test-apparatus before the choice. This learning may have occurred when the bird pecked at the bridge or at its feet. In this case the learning-process would have to occur very quickly, perhaps facilitated by the fact that in other respects the subjects were not sensorially deprived.

Choice-trials with subjects which had been exposed.

The differences are such that Se and De tend to choose in accordance with the type of exposure previously administered, and the control-group in apparent accordance with an inborn tendency. The basis of the tendency here to choose the previously exposed side is not quite clear, although it can be assumed that De is in conflict between an inborn tendency and the early experience of depth.

Thus, in the exposure-groups the results may be interpreted as a conflict between rival learning-signals. Besides the depth itself, the animals should also have been accustomed by then to the visual cues emerging from their feet. This would mean that in the Se-groups cues from the glass-surface on the deep side could have given rise to some wrong choices if the depth below was not

sufficiently noticed. In the De-group, in line with the hypothesis just mentioned, it is quite to be expected that a number of subjects should also choose the shallow side, since it is at the same height as the level of the feet (i.e. during the period of choice or of exposure the signals from the deep side may not have been sufficiently noticed) (cf. Tallarico & Farrell, 1964; Carr & McGuigan, 1965).

Time-variables: The simplest explanation of the importance of long (24 hr) exposure is that it gives the animals time to learn. This may also provide them time to overcome the confusing conflict between inborn tendency and early learning.

In addition, it enables the animals to overcome a conflict between rival learning-signals (from lower plane and the foot-plane respectively), to become accustomed to the double aspects of its situation and regard this as normal.

The significant differences from the 0-interval are perhaps due to the fact that exposure here is immediately prior to testing. The interval 1-24 hours seems to be a period of consolidation. After this the effect of the exposure again shows up clearly. Thus, the similarities of results by the 0-interval and the >24-hours interval can perhaps be explained in terms of a U-type relationship between learning and length of interval.

Latency-times: In Table III it is evident that the "wrong-choice" groups (SeDc and DeSc) have made hasty (and presumably ill-considered) choices. A difference in latency-times shows up most clearly between the groups SeSc/SeDc (SeSc>SeDc). Neither of these two groups would appear to have been in a conflict of the kind mentioned earlier (i.e. between either inborn tendencies and learning or between rival learning-signals), since both groups are exposed on the shallow side. Provided they recognized the alternatives correctly their choices should thus have been correct. That group which failed to make correct choices (group SeDc) has considerable shorter latency-times. A possible interpretation would be that this is the more emotional or impulsive group. A similar interpretation could be invoked for the difference DeDc>DeSc. The difference also found of DeDc>SeDc can be explained in terms of greater conflict and/or less impulsiveness in the former group.

Other behavioral manifestations: In the same manner, the difference for the pluming-variable of SeSc>DeDc can be interpreted in terms of conflict in the group DeDc, its being assumed that birds who are in conflict plume themselves less. In comparing the groups Se and De we can note this phenomenon again: the De-groups have lower values.

The difference in pluming behavior DeSc>DeDc does not achieve significance. It fits rather well, however, with what was shown before. According to our previous assumptions, exposure has no particular effect on DeSc. As just

discussed, this group also tends to perform hasty, apparently ill-considered choices. Since they thus appear to escape conflict by making quick decisions, their pluming behavior can be interpreted in terms of reflecting less conflict than that of the group DeDc.

The difference in pluming behavior $SeSc > SeDc$ is rather slight but SeDc also performs more "wrong" and hasty choices and thus appears to be more impulsive than SeSc. Possibly alarm-factors may be involved.

Interpretation of the oscillation-variable seems straightforward enough. According to what has been said already, the De-groups are in conflict (between inborn tendencies and learning or between rival learning signals). If it be assumed that subjects in conflict oscillate more, this interpretation is in line with the differences found, where $De > Se$, $DeDc > SeSc$ and $DeSc > SeSc$. In addition, the differences $SeDc > SeSc$ and $Right-c < Wrong-c$ may also be based on the avoidance of conflict, i.e. an alarm reaction accompanied by rapid choice. It would seem there should also be a difference $DeDc > DeSc$, since according to our reasoning DeDc is the most conflict-loaded group. Although this difference is not found, both of the groups are conflict-loaded and the sample is small.

The difference in the oscillation-variable $DeDc > SeSc$ could have been expected to be larger than was the case, since DeDc is the most conflict-loaded and SeSc the most conflict-free group. Chance-effects can be considered here also.

The differences in the pecking-variable, weak as they are, do not appear amenable to interpretation.

Since the differences with the looking-variable $DeDc > SeSc$ are found in the ten-minute period around the choice, this may indicate that $DeDc$ looks around more closely before choosing. This fits our conflict-theory, for if $DeDc$ is the more conflict-loaded group, these subjects ought reasonably to inspect the sides more carefully before choosing. This is in accordance with the results for the pluming-variable although disagreeing in part with those of the oscillation-variable.

C o n c l u s i o n s

The results indicate that an organism with suitable training prefers depth to shallowness. This may be interpreted on the basis of two models:

A. An inborn tendency exists to choose the shallow side, this tendency later being modified during exposure. This is a fully developed system already present at birth, but a system which it is possible to modify.

B. Only a basic structure exists at birth. With experience (exposure) the system becomes complete. This process occurs very quickly and probably only early in life. Perhaps it is a question of structural cell-organisation.

"A" links up with our reasoning regarding a conflict between inborn tendencies and learning, and "B" with that regarding conflict between rival learning-signals.

When considering the wrong or partially wrong choices in the DeSc and SeDc groups, one should also consider the possibility of alarm factors, as was mentioned above.

R e f e r e n c e s

- Carr, W.J. & McGuigan, D.I. (1965). The stimulus basis and modification of visual cliff performance in the rat. Anim. Behav., 13, 25-29.
- Emlen, J.T. Jr. (1964). Determinants of cliff edge and escape responses in Herring Gull chicks in nature. Behaviour, 22, 1-15.
- Fabricius, E. (1951). Zur Ethologie junger Anatiden. Acta Zool. Fenn., 68, Helsingfors: Societas pro flora et fauna fenn.
- Gibson, E.J. & Walk, R.D. (1960). The "Visual cliff". Sci. Am., 202, 64-71.
- Kurke, M.I. (1934). The role of motor experience in the visual discrimination of depth in the chick. J. genet. Psychol. 86, 191-196.
- Lashley, K.S. & Russel, J.T. (1934). The mechanism of vision: XI. A preliminary test of innate organisation. J. genet. Psychol., 45, 136-144.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vögels. Ibid, 83, 137-213, 289-413.
- Pumphrey, R.J. (1948). The sense organs of birds. Ibis, 90, 171-199.
- Russel, J.T. (1932). Depth discrimination in the rat. J. genet. Psychol., 40, 136-159.

- Thorndike, E. (1899). The instinctive reactions of young chicks. Psychol. Rev., 6, 282-291.
- Tallarico, R.B. & Farrell, W.M. (1964). Studies of visual depth perception: an effect of early experience on chicks on the visual cliff. J. comp. physiol. Psychol., 57, 94-96.
- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press.
- Walk, R.D. & Gibson, E.J. & Tighe, A.T.J. (1957). Behavior of light- and darkreared rats on a visual cliff. Science, 126, 80-81.
- Walk, R.D. & Gibson, E.J. (1961). A comparative and analytical study of visual depth perception. Psychol. Mon., 75, No. 15, 1-44.

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*Colour Structures and Extinction of Aggressive Display
in the Male Three-Spined Stickleback (*Gasterosteus
aculeatus* L.)*

by S. Birger Hansson, Birgitta Holmqvist and Inga-Britt Strömberg



LUND UNIVERSITY SWEDEN

A b s t r a c t. - The reactions of ten male three-spined sticklebacks to conspecific models was investigated. The goal was to find out which if any of the colour-structures during spawning evoke territorial fight and if these responses can be extinguished. The results indicate that both the red belly and the blue eye are effective stimuli. Extinction was successful although recovery occurred.

In its ease in handling, its ready accessibility and its richly developed behaviour pattern during spawning the three-spined stickleback has become one of the classical experimental animals in ethology (Tinbergen, 1952).

Actually the three-spined stickleback is a shoe-animal, but when the spawning begins the shoe scatters and the male selects a part of the bottom to be his own and to maintain as territory. Here he builds a nest and thereafter engages in the complicated interplay between male and female which leads to spawning and fertilization. The female is then hunted away from the territory and the male cares for the offspring (Tinbergen, 1951).

When males of the same species intrude upon the territory they are treated with hostility. Their colour-structures appear to play an important role in evoking this territorial-fight. Normally the three-spined stickleback is silverly coloured, the female remaining so even during spawning. At the beginning of the latter, however, the male undergoes a colour-metamorphosis which results in a beautiful dress with red belly, silver-blue back and a clearly shining blue iris. Previous research has attempted to simulate mature, spawning animals with dummies and to test

different components of dress and behaviour; the red colour has appeared here to be the signal evoking the territorial-fight (Pelwijk & Tinbergen, 1937).

In the experiments supposedly demonstrating this, however, not much attention seems to have been paid to the blue iris. During our preparatory tank-observations we could not avoid wondering what significance such a prominent structure might have since it appeared to us that during territorial fighting the males repeatedly bit directly at the eyes, we posed first the following question:

(A) Has the blue iris of the male three-spined stickleback any signal-function in evoking territorial-fight responses?

If we made use of the method of extinction, we could perhaps obtain an answer to an additional problem, namely how deeply rooted in the behavioural repertoire of these animals territorial fighting is, and what procedures could be used to provide a measurement of the signal-strength of each tested colour-structure. This led us to our second question:

(B) Is it possible to extinguish responses to a stimulus-situation which usually evokes territorial fighting and if so is there any correspondence between rate of extinction and the kind of colour-structure?

S u b j e c t s

Ten male three-spined sticklebacks (*Gasterosteus aculeatus* L.) were employed as experimental subjects. The fish were captured in a small creek outside Trelleborg (southern Sweden) at the beginning of May. Spawning had not yet begun, possibly because of an extremely long winter in 1970, which had delayed mating. The first captured individuals needed approx. 14 days until any sign of mating appeared. The fish were fed with *Daphnia*.

Concerning colour vision in these fish all facts point to its existence since other teleosts - to which this species belongs - have been found to possess it (e.g. Jacobson, 1968). They seem to experience hue as a quality of sensation apart from brightness (Walls, 1942), and their visual system gives some chromatic response to every visible wavelength (Yager, 1968).

A p p a r a t u s

Immediately after capture the fish were placed and kept in darkened aquarium. Three 90 liter plexiglass aquariums were used for testing. Each of these was divided with the help of glass-sheets into four compartments measuring 17.5 x 35 x 35.5 cm.^x The bottom was covered with a layer of fine sand several cm thick. Some pebbles and a plant with foliage were places in each compartment. There was also straw-like material for nest-building. The walls were carefully kept clean of algae. Oxygen was supplied with the help of a large airpump connected to plastic tubes and distributing oxygen evenly between the compartments. The water-temperature was successively raised during the course of several days from appr. 14° when the fish were first placed in their compartments to appr. 20°, being kept constant during testing. Fluorescent tubes supplying 1400 lux were placed above the aquariums. They were shut off for four hours during the dark period of the day. The laboratory was otherwise in darkness (cf. Reventlow, 1970).

Three dummies of 3 mm thick transparent plastic were used for testing (Fig. 1). They were handled with the help of a steel-wire fastened in a hole in the back of the dummy. Glossy colour-paper was attached to the dummies. One of

^xAccording to a recently published field-study, nests and natural conditions seem not to be closer than 30 cm, the mean distance being 73 cm (Black & Wootton, 1970). In our situation it has been possible to reduce the area of territory, probably thanks to the glass-sheets preventing the fish from attacking each other.

the dummies was furnished with a red belly (R-11-20)⁺, the second had the same red belly plus a blue eye (Bq-6-12-22)⁺ 4 mm in diameter, and the third was furnished only with a grey belly (G-10)⁺. Finally the dummies were treated so that the paper would stand moisture.

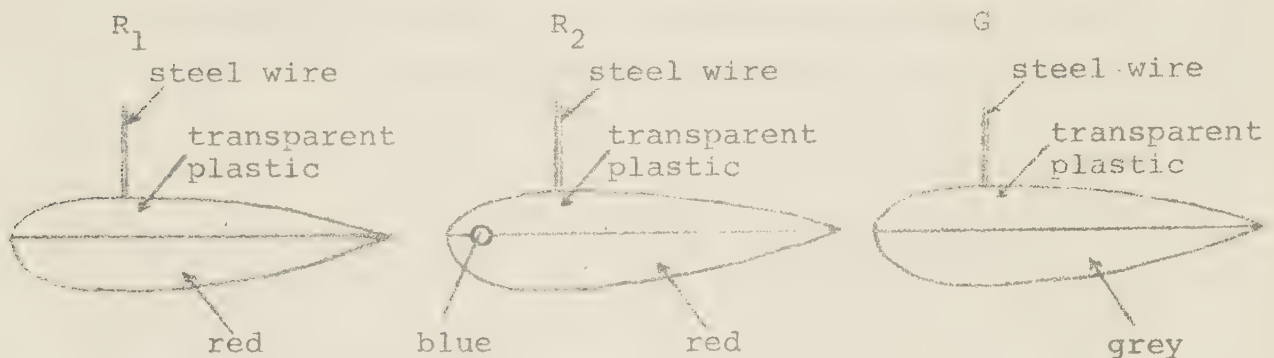


Fig. 1. The dummies in their natural size.

Procedure

Before testing, two sheets of opaque glass were sunk down along opposite sides of the chamber in question to isolate it visually from the neighbouring chambers.

The dummies were lowered into the water at an even and rather low speed. One of the opaque sheets functioned as background, usually in that part of the chamber where the fish had its nest.

During each presentation coded registrations of behaviour were made. No behavioural manifestations were recorded, however, during the moving of the dummy - this to avoid

⁺Hesselgren's notations, AB Colour Center, Bromma, Sweden.

Table I. The complete schemes for randomization of the stimuli. Note that entering of the design is randomly distributed among the rows.

R ₁	R ₂	G	R ₂	G	R ₁	G	R ₁	R ₂
R ₂	G	R ₁	G	R ₁	R ₂	R ₁	R ₂	G
G	R ₁	R ₂	R ₁	R ₂	G	R ₂	G	R ₁

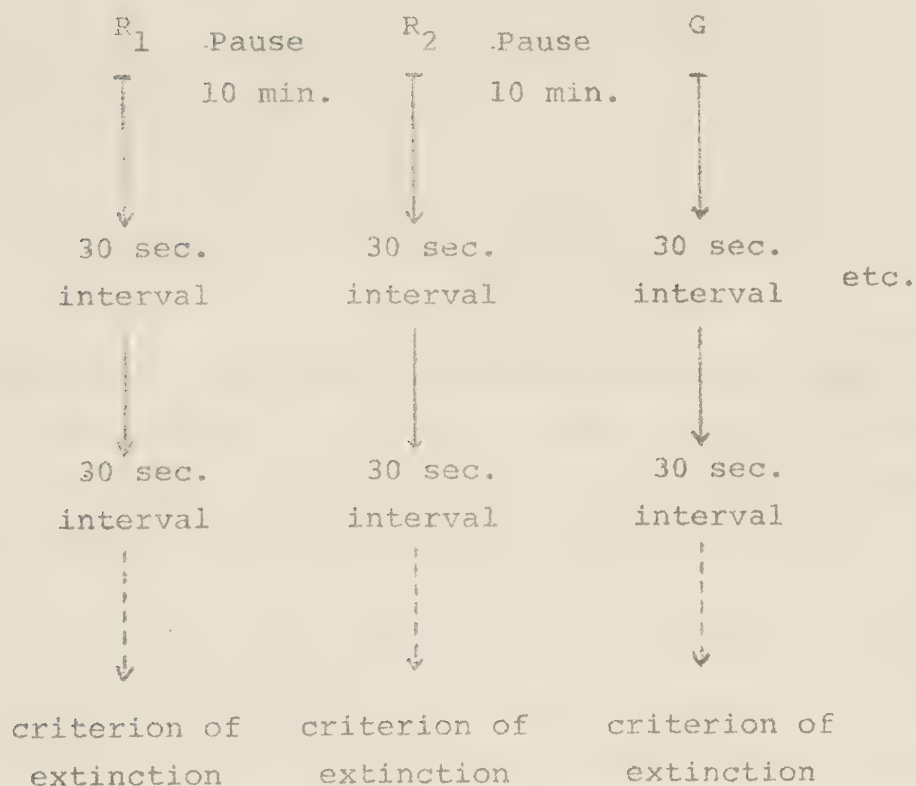


Fig. 2. Time sequence within one of the schedules of presentation.

interference in the form of movement-components. The behavioural manifestations were divided into two categories:

Behavioural manifestations tentatively classified as aggressive: biting, hunting, releasing stickles, vertical position and sand-spitting.

Possibly non-aggressive manifestation of behaviour: fanning, mirror-swimming and zigzag-dance.

Legend: Biting: attempting to cut into the dummy; hunting: self-propulsion against the dummy; releasing stickles: releasing of side- and back-stickles; vertical position: stands vertical to the bottom; fanning: supplies water to the nest with the help of the fins (belongs actually to the care of the offspring); mirror-swimming: follows its own mirror-picture up and down along the reflecting glass side; zigzag-dance: zigzag-movements (actually part of mating) (cf. Pelwijk & Tinbergen, 1937; Tinbergen, 1951; Sevenster, 1961; van den Assem & van der Molen, 1970).

D e s i g n

Each dummy was presented to the animal for successive 30-second periods following pauses of 30 seconds each until a criterion of extinction was reached; five "0-periods" in a row was considered as the criterion (0-period: a period without any responses tentatively classified as aggressive). Following this procedure there was a pause of ten minutes until the next stimulus was shown (Fig. 2). The stimuli were presented in accordance with a balanced scheme (Table 1). When each of the stimuli had been presented three times, testing was broken off until the following day when it was resumed in the same manner and at the same time of day. Thus, a complete series of testings, i.e. 12 extinction-series with the same stimulus, took 4

days to complete. At testing the fishes were in different stages of nest-building.

R e s u l t s

An extremely low frequency of response in five of the subjects forced us to base the analysis of results on data from only the five remaining ones, which had sufficient total frequencies.

Number of aggressive responses

Number of non-aggressive responses

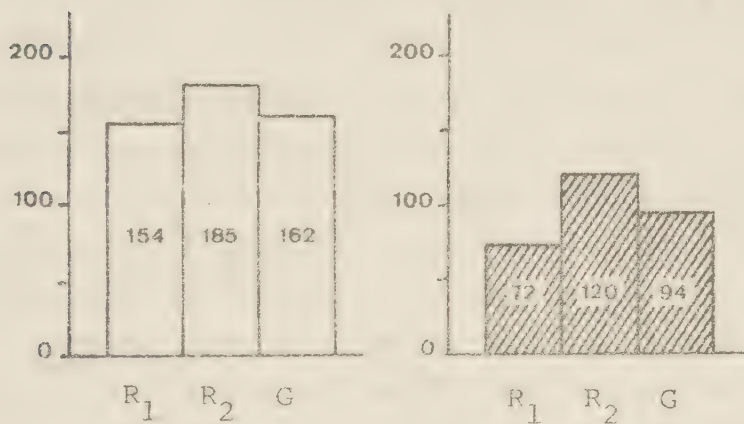


Fig. 3. The total frequency of aggressive and non-aggressive responses to stimuli R₁, R₂ and G.

The total number of responses to the different dummies - without dividing the responses into the categories aggressive/non-aggressive: A significant difference between the dummies was shown in that R₂ received the most responses there ($\chi^2 = 12.2$, $p < 0.01$, df 2, or Friedman: $\chi^2_r = 6.16$, $p < 0.05$). The main difference appears to be the one between R₁ and R₂ (Wilcoxon: $T = 11$, $N = 11$, $p = .025$, one-tailed).

The total number of responses to the different dummies - (A) aggressive and (B) non-aggressive responses being distinguished (see Fig. 2): (A) No significant difference between the three dummies could be shown, however, there was a trend evident of R_2 receiving the most responses ($\chi^2 = 3.53$, $p = 0.15$, $df\ 2$). Paired comparisons revealed a significant difference between R_1 and R_2 (Wilcoxon: $T = 11$, $N = 11$, $p = .025$, one-tailed).

(B) A significant difference was found between the three dummies, R_2 receiving the most responses ($\chi^2 = 11.3$, $p < 0.01$, $df\ 2$). No significant difference was found in paired comparisons of the different dummies.

The total number of periods with or without aggressive responses (see Table II): A significant difference was found between the three dummies, where $\chi^2 = 9.48$, $p < 0.01$ ($df\ 2$), R_2 receiving the most periods with an aggressive response, and also (since the total number of responses to this dummy was greatest: see above) the most periods without aggressive response. The former is statistically significant ($\chi^2 = 5.99$, $p = 0.05$, $df\ 2$); the latter is not.

Table II. The total number of periods with aggressive response or without.

Stimuli	R_1	R_2	G
Number of periods with an aggressive response	80	114	96
Number of periods without aggressive response	51	84	70

The number of aggressive or non-aggressive responses during the first and the second half of each test period respectively (see Table III): Significant differences were found, the first half containing more aggressive (and fewer non-aggressive) responses than the second half (see Table II; $\chi^2 = 11.9$, $p < 0.001$, $df\ 1$, and Wilcoxon: $T = 1$, $N = 8$, $p < 0.01$, one-tailed), this being for all three stimuli taken together. If we consider each stimulus alone we find a significant difference for R_1 ($\chi^2 = 10.7$, $p < 0.01$, $df\ 1$) and for R_2 ($\chi^2 = 9.46$, $p < 0.01$, $df\ 1$).

Table III. The number of aggressive and non-aggressive responses during the first and second half of the test period respectively.

	First half of the test-period	Second half of the test-period
Aggressive responses	229	191
Non-aggressive responses	102	150

Extinction

The number of aggressive responses to the different dummies: (see Fig. 4). Correlation between the order of presentation and the frequency of responses yields significant differences in two cases, namely for R_2 ($r_s = -0.77$, $p < 0.01$) and for G ($r_s = -0.53$, $p < 0.05$).

For a comparison of the frequencies of response for the different occasions of presentation we summed the frequencies of response for all the first presentations over

the four days, and for all the 2nd and 3rd presentations accordingly (see design). The summed frequencies of response were significantly greater for the first presentations than for the others (see Fig. 4), this was true, for all the dummies (R_1 : $\chi^2 = 190.2$, $p < 0.001$, $df\ 2$; R_2 : $\chi^2 = 103.9$, $p < 0.001$, $df\ 2$; G : $\chi^2 = 112.0$, $p < 0.001$, $df\ 2$).

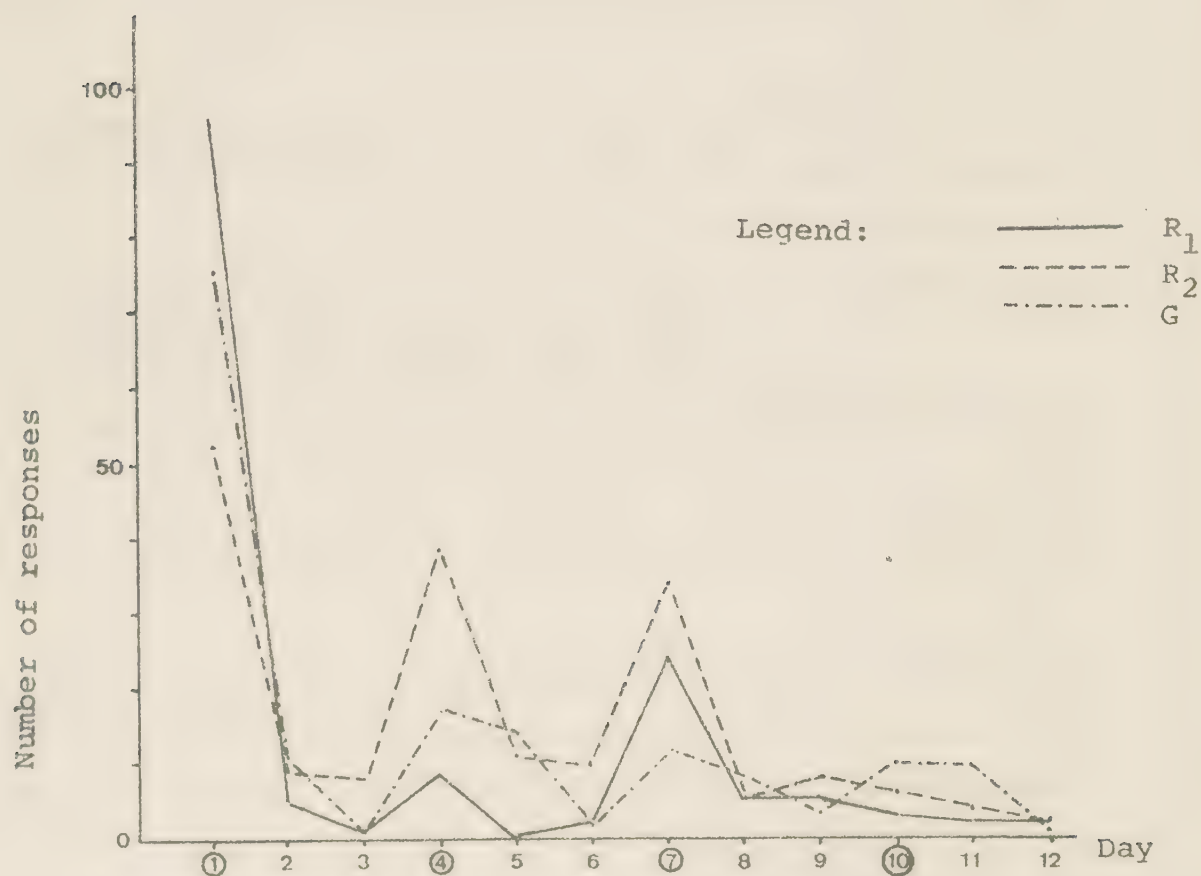


Fig. 4. Extinction over days of aggressive responses (first daily presentations indicated by circles).

The number of non-aggressive responses to the different dummies (see Fig. 5): the correlation between the order of presentation and the frequency of response is also significant for R_2 ($r_s = -0.59$, $p < 0.05$) and for G ($r_s = -0.58$, $p < 0.05$).

For a comparison of the frequencies of response for the different occasions of presentation here we proceeded in the same manner as with the number of aggressive responses (see above). The summed frequencies of non-aggressive responses were significantly greater for the first presentations than for the others (see Fig. 5), this being the case for all the dummies (R_1 : $\chi^2 = 52.9$, $p < 0.001$, $df\ 2$; R_2 : $\chi^2 = 19.1$, $p < 0.001$, $df\ 2$; G : $\chi^2 = 38.5$, $p < 0.001$, $df\ 2$).

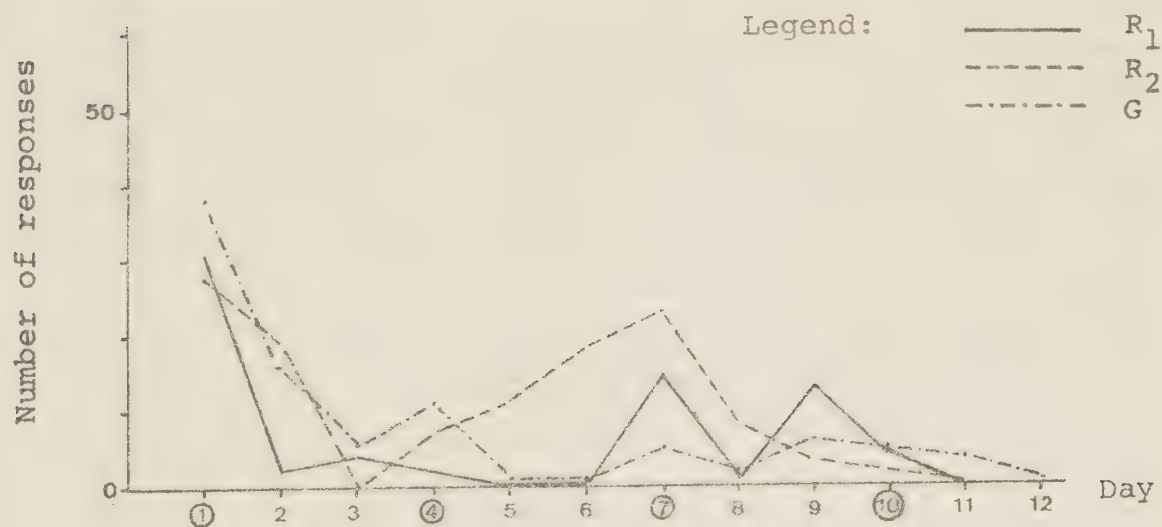


Fig. 5. Extinction over days of non-aggressive responses (first daily presentations indicated by circles).

Discussion

The low response-levels of the five individuals that were discarded may be due to low motivation since these fish were tested at the end of the spawning-period (which was indicated by their poor colouration). Considering this, their response-level would tend to confirm what earlier research has indicated concerning the importance of an optimal state of motivation (Tinbergen, 1951; cf. Peeke, Wyers and Herz, 1969 concerning "non-responders").

Response strength

In general R_2 evokes the greatest number of responses and seems therefore to be the stimulus evincing the greatest excitation. It is interesting, however, that there is a significant difference between R_1 and R_2 , while R_2/G and R_1/G do not show any significant difference. This was not to have been expected on the basis of earlier research; in fact the grey dummy (G) lacks all signal properties - aggressive as well as sexual ones (Pelwijk & Tinbergen, 1937; Tinbergen, 1951). On the other hand van Iersel has reported aggression toward the female during the phase of nest-building (van Iersel, 1953). This is contradicted by Reventlow, however, who did not find such tendencies in his sample (Reventlow, 1970). Another recent report indicates that fish tested before nest-building show as aggressive behaviour toward non-gravid females as toward males. After completion of the nest they are more aggressive towards males (Wootton, 1970). These findings may partly explain the data concerning the grey female-like dummy reported above, since not all of our fish had completed their nests at testing. If so, however, it would seem hard to explain the proposed shift in aggression. It may be that gonadal

hormones increase the sensitivity of the male to red (Wootton, 1970). But no evidence of a spectral shift in sensitivity in the male stickleback has been found (Cronly-Dillon & Sharma, 1968). In any case each of the dummies seems here to have some exciting effect, even if it seems most evident for R_2 .

Furthermore, R_2 seems to evoke more aggressive responses than the other two stimuli. This can be viewed as supporting our assumption that the blue iris has some signal function in evoking responses which belong to the territorial-fight, but contradicts earlier research which has indicated the red belly (R_1) to be the most effective stimulus and be sufficient to evoke territorial fighting (Pelwijk & Tinbergen, 1937). The matter is complex, however, since R_2 also evokes more non-aggressive responses than the other two dummies.

In this connection it is interesting to note that R_1 (the stimulus of the red belly only) elicits the smallest number of aggressive responses. This would definitely not be expected on the basis of earlier research (Pelwijk & Tinbergen, 1937; Tinbergen, 1951).

Even if the total number of periods with an aggressive response or without is counted, R_2 is the most effective stimulus. This is also true if only the number of periods with an aggressive response is counted. This confirms what was said earlier about R_2 being the stimulus causing the greatest excitation and most effective in evoking aggressive responses.

With regard to the number of aggressive/non-aggressive responses during the first and second half of the test-period respectively, there is great difficulty in classifying the responses. Our dichotomizing took place after thorough observation of responses to the dummies as well as to living fishes and agrees in principle with earlier research. It is confirmed by the data here to the extent that it seems reasonable to assume that the aggressive responses occur at the beginning of each presentation and later decrease due to the dummies not giving proper feedback stimulation.

If we consider the aggressive and non-aggressive responses to each stimulus, we find significant differences for R_1 and R_2 . This suggests that aggressive responses to R_1 and R_2 are of a different kind than those to G. Probably G has more of an over-all effect eliciting elements of aggressive motivation, but one possibly not as specific as with R_1 and R_2 .

Extinction

Concerning the aggressive reactions, the negative correlations between the order of presentation and the frequencies of response indicates that R_2 and G evoke more responses at earlier occasions of presentation than at later ones. This applies to a lesser degree to R_1 also (cf. Fig. 4). Thus, there seems to be some extinction over days, of the responses belonging to territorial-fight (cf. Peeke, Wyers & Herz, 1969; van den Assem & van der Molen, 1969).

During each day there is a striking extinction to all stimuli. In accordance with what is to be expected from an

extinction phenomenon, spontaneous recovery also occurs (Thompson & Spencer, 1966). This may indicate that the behaviour in question is rather strongly rooted in the behavioural repertoire of the subjects.

As for the non-aggressive responses, these also show extinction, both over the days and within each day. Spontaneous recovery, however, is not so marked as for aggressive reactions.

C o n c l u s i o n s

If we attempt to answer question (A) set in the introduction we may consider two possible answers:

(i) The blue iris seems to have some signal-function in evoking territorial-fight since the dummy with the red belly and the blue eye (R_2) evokes more aggressive reactions than the other two. This is in accordance with what has been said about "heterogeneous stimulus summation" (Seitz, 1940; Tinbergen, 1948). But since it also evokes more non-aggressive reactions, the effect of the stimulus may be both an increase in action-potential and an increase in aggressive motivation. That these two functions should be connected seems reasonable on the basis of some earlier reports (e.g. Brown, 1961) but is contradicted by Tinbergen (Tinbergen, 1951).

Answer (i) also seems plausible if one consider how the selection might have worked. If the blue eye had no signal-function of value for survival of the species, the blue colour should have faded, vanished or not appeared at all.

(ii) The dummy with the blue eye (R_2) evokes more responses since it constitutes a more structured stimulus and has greater attention value. Its effect thus appears to be simply that of heightening action-potential. This reasoning finds some support in the investigation if we consider the definite role which the grey dummy (G) seems to have played.

If we consider how selection may have worked, it would be reasonable to suppose that the blue of the eye might also be connected with some other function of importance for the survival of the species.

On the other hand, the difference in the number of aggressive responses during the first and second half of the testperiod respectively between the coloured stimuli (R_1 and R_2) and the grey dummy (G) seems hard to explain on the basis of answer (ii).

According to answer (ii), neither the red belly nor the blue eye colour has any signal-function in evoking territorial-fight; this conclusion contradicts earlier research (above all Pelwijk & Tinbergen, 1937).

In considering our question (B), it seems that extinction takes place, and that this is most marked for the aggressive responses. Thus, we are faced with a modification of a type of behaviour having great survival value for the species, as the avoidance of depth by young eiders shown in previous research (Hansson, 1970).

The extinction appears to indicate that the relation between

sign-stimulus and the strength of response is more complicated than Tinbergen supposed (Tinbergen, 1951). The curves of aggressive reactions are in fact quite like ordinary extinction-curves (Thompson & Spencer, 1966), and the decreasing responsiveness cannot depend on muscle-exhaustion since after extinction the subjects still react to other stimulation. Neither could it be explained with reference to discharge of some "central nervous energy" (Lorenz, 1950), since the long-lasting process of extinction makes that improbable. It may rather be that the responses belonging to the territorial-fight are flexible open to different kinds of learning processes.

R e f e r e n c e s

- Assem, J. van den & Molen, J.N. van der (1969). Waning of the aggressive response in the three-spined stickleback upon constant exposure to a conspecific. I, a preliminary analysis of the phenomenon. Behaviour, 34, 286-324.
- Black, R. & Wootton, R.J. (1970). Dispersion in a natural population of three-spined sticklebacks. Canad. J. Zool., 48:5.
- Brown, J.S. (1961). The motivation of behavior. New York: McGraw-Hill.
- Cronly-Dillon, J. & Sharma, S.C. (1968). Effect of season and sex on the photopic sensitivity of the three-spined sticklebacks. J. exp. Biol., 49, 679-687.
- Hansson, S.B. (1970). Visual depth discrimination in young eiders (*Somateria mollissima*). Psychol. Res. Bull., Lund Univ., X:13.

- Iersel, J.J.A. van (1953). An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour, suppl., 3, 1-159.
- Jacobson, M. (1968). Physiology of fish vision. In D. Ingle (Ed.). The central nervous system and fish behavior. Chicago and London: Univ. of Chicago Press.
- Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. Symp. Soc. exp. Biol., 4, 221-268.
- Peeke, H.V.S., Wyers, E.J. & Herz, M.J. (1969). Waning of the aggressive response to male models in the three-spined stickleback (*Gasterosteus aculeatus* L.). Anim. Behav., 17, 224-228.
- Pelwijk, J.J. ter & Tinbergen, N. (1937). Eine Reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. Zeitschr. f. Tierpsychol., 1, 193-201.
- Reventlow, I. (1970). Studier av komplicerede psyko-biologiske fœnomener. Copenhagen: Munksgaard.
- Seitz, A. (1940). Die Paarbildungen bei einigen Cichliden I. Zeitschr. f. Tierpsychol., 4, 40-84.
- Sevenster, P. (1961). A causal analysis of displacement activity (fanning in *Gasterosteus aculeatus*). Behaviour, suppl., 2, 1-170.
- Thompson, R.F. & Spencer, W.A. (1966). Habituation: a model phenomenon for the study of neuronal substrates of behaviour. Psychol. Rev., 73, 16-43.
- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press.
- Tinbergen, N. (1952). The curious behavior of the stickleback. Scient. Am., 187, 22-26.

- Walls, G.L. (1942). The vertebrate eye. Michigan: Crambrook Institute of Science.
- Wootton, R.J. (1970). Aggression in the early phases of the reproductive cycle of the male three-spined stickleback (*Gasterosteus aculeatus*). Anim. Behav., 18, 740-746.
- Yager, D. (1968). Behavioral analysis of color sensitivities in goldfish. In D. Ingle (Ed.). The central nervous system and fish behavior. Chicago and London: Univ. of Chicago Press.

THE INFLUENCE OF STIMULUS CONTRAST ON THE AGGRESSIVE DISPLAY
OF THE MALE THREE-SPINED STICKLEBACK (*Gasterosteus aculeatus*
L.)

by

S. Birger Hansson

Lund, 1973

A b s t r a c t . - The author investigated the aggressive reactions of male three-spined sticklebacks to fish-like models possessing different degrees of brightness contrast. The model with the highest intra-stimulus contrast got the most aggressive responses. The result was interpreted as indicating the importance of considering degree of structure of presumed sign-stimuli.

I n t r o d u c t i o n

It was expressed rather early within classical ethology represented e.g. by Konrad Lorenz and Niko Tinbergen that the extrinsic stimulation sufficient to trigger a so-called Innate Releasing Mechanism (IRM) should be of a very special kind. It was further postulated that the stimulus should correspond to "preformed neural mechanisms", and should fit like a key in a lock (Lorenz, 1935, 1950; Tinbergen, 1942, 1951).

The effective stimulus in the environment was called "Sign Stimulus" by Tinbergen^x, and its function was illustrated in the aggressive display of the three-spined stickleback:^{2x}

"... the fish reacted essentially to the red and neglected the other characteristics. Yet its eyes are perfectly able to 'see' these other details" (Pelwijk and Tinbergen, 1937; Tinbergen, 1951).

The assumption that the display of specific extrinsic structures under certain circumstances may evoke adaptive behaviour has been integrated with evolutionary theory (e.g. Lorenz, 1939). Further sign stimulus was given a crucial role in the formulation of the motivational theories by Lorenz (1950) and Tin-

^x The terms suggested by Tinbergen will be used throughout this study. For the corresponding terms of Lorenz and for a comparison between the model of Lorenz and that of Tinbergen see Schleidt (1962).

^{2x} The behaviour of the three-spined stickleback is described elsewhere (see e.g. van dem Assem, 1967, and for a brief introduction, Tinbergen, 1952).

bergen (1951). On the descriptive level the heuristic value of the concept has been great in generating numerous studies searching for different sign stimuli in different species. Finally, regarding development, reactivity to certain sign stimuli (such as the red belly of the male stickleback) in the specific situation of the deprivation experiment has been given the status of crucial proof of the existence of innate behaviour (Lorenz, 1965).

Early, the concept of sign stimulus was extended to explain phenomena such as stimulus summation, configuration of features and differentiation between innate and conditioned perception (e.g. Tinbergen, 1951). Underlying this is the suggestion that innate sign stimuli have simple and distinctive features (Lorenz, 1939).

Although the idea that certain movements and structures have a message carrying function is thus established in ethology (Baerends, 1950), the concept of sign stimulus has several times been criticized especially from a developmental and methodological point of view by e.g. Lehrman, 1953; Marler, 1961; Hinde, 1966.

Regarding the ethology of the three-spined stickleback, difficulties in obtaining unanimous identifications of stimuli as sign stimuli are illustrated by some studies failing to confirm the classical notation of "red underneath" as constituting the most potent stimulus for the male reproductive aggression (Muckensturm, 1968; Peeke, Wyers and Herz, 1969).

In a previous study of aggressive display in the male three-spined stickleback (Hansson, Holmqvist and Strömberg, 1971), we found that a dummy with a red belly and blue eye was attacked more often than a dummy with a red belly only (although the blue eye was considered a stimulus-aspect of minor importance by Tinbergen, 1953).

We recognized that our findings could be explained in two different ways:

- (1) The preference for the stimulus configuration "red belly and blue eye" could constitute a case of heterogenous stimulus summation (Seitz, 1940; Tinbergen, 1948), which, as was noted earlier, is an extension of the original meaning of sign stimulus.
- (2) The configuration of blue and red could constitute a superior stimulus in evoking aggressive responses since it was better structured and therefore commanded more attention.

Furthermore in our study 1971 we also reported a high proportion of aggressive responses directed against a grey dummy (resembling a female). In a similar way Wootton (1970) had found that during the first period of the reproductive cycle (the prenest phase) the male stickleback tends to attack both males and females, and the same phenomenon was reported by van Iersel (1953) regarding the nest-building phase. These findings may depend on the fact that the sight of a completed nest releases the sensitivity to the red belly; it may also be that the role of a specific hue in the releasing process has been overestimated.

In order to test whether coloured fish were attacked more often because of their clearer structure (thus their higher attention value), an experiment was designed to avoid all features in the stimulus situation which could be referred to as sign stimuli. As in the previous study the fish were presented with constant stimuli, but this time the dummies lacked all colour. Each dummy presented a randomized pattern of different shades of grey ranging from black to white. The different shades were distributed randomly on the dummies since for colour position has also been given the status of a sign stimulus (Tinbergen, 1948).

The relative degree of brightness contrast within the stimulus has been considered to be an index of stimulus structure. A stimulus with high intrastimulus contrast is therefore thought to be more structured, and to possess a higher attentional value than a stimulus with low intrastimulus contrast.

Since we regarded the process of habituation as an effective measure in determining the power of each stimulus in eliciting attacks, the following hypothesis was formulated:

The males make the most intense and frequent attacks on the stimulus with the highest degree of intrastimulus structure; that is, the stimulus with the highest degree of brightness contrast. The intensity of attacks will co-vary with the speed at which the aggressive behaviour habituates within each test-session and over days.

A n i m a l s

15 male three-spined sticklebacks (*Gasterosteus aculeatus* L.) were used. The fish were captured in the harbour of Limhamn outside Malmö, in southern Sweden) in the beginning of October. They adapted to fresh water within two days, and mated within four weeks. The fish were fed partly with tubifex and partly with granulated salmon fodder^x. They were tested during the prenest phase.

E q u i p m e n t

Three 100 l plexi-glass aquaria were used for the testing. Each of these was divided with the help of opaque glass sheets into four compartments measuring 17.5 × 35 × 35.5 cm. The bottom of each aquarium was covered with sand and pebbles, and a plant with foliage was placed in each compartment. Oxygen was supplied.

The water temperature was kept constant at approximately 20°C. Fluorescent tubes supplying 1400 lux were placed above the aquaria. In order to get the animals into display the lights were shut off for only two hours during the dark period of the day (Reventlow, 1970).

Four dummies made of 3 mm thick transparent plastic were used as stimuli. They were handled by means of a steel wire fastened to the back of the dummy. Glossy coloured paper in two

x

Astra - Evos AB, Södertälje, Sweden.

achromatic colours was attached to each dummy in a random pattern (covering the whole dummy). One of the stimuli (S_1) was supplied with white and black paper (1M+24M)^x, S_2 with very light and dark grey paper (4M+16M), S_3 with light and full grey (6M+12M) and S_4 with unitary grey (8M+8M). The shape of the dummies was that of a natural fish.

P r o c e d u r e

The dummies were lowered into the water at an even and rather low speed usually near the middle of the chamber. No registrations of behaviour were made during the movement of the dummy.

Behaviour was classified into aggressive and non-aggressive categories (Hansson et al., 1971). The terminology used in our 1971 study was partially replaced with terms suggested by van Iersel (1953). We exchanged the terms releasing stickles, hunting, vertical position, sand collecting and mirror swimming for spine erection, charge, threatening, bringing sand and fluttering, respectively.

Biting, charge, spine erection and threatening were judged as aggressive. Bringing sand, fluttering and zig-zag dance were judged as non-aggressive (for a description of these terms see van Iersel, op.cit. and Hansson et al., op.cit.).

D e s i g n

Each dummy was presented for successive 30-second periods followed by pauses of 30 seconds each, until a criterion of habituation was reached. This criterion was five 0-periods in a row (0-period: a period without any aggressive responses). Following this procedure there was a pause of ten minutes until the next stimulus was shown (see also Hansson et al., 1971).

The stimuli were presented in a latin square design in which their order of presentation was systematically varied (Cohran and Cox, 1957).

A n a l y s i s o f r e s u l t s

An extremely low frequency of response in five of the subjects forced us to exclude them from the analysis. The case of non-responders is not unusual (c.f. Peeke, Wyers and Herz, 1969) and the underlying factors has been discussed elsewhere (Hansson et al., op. cit.; Tinbergen, 1951).

^x Hesselgrén's notations, AB Colour Center, Bromma, Sweden.

In general there were very low frequencies of non-aggressive responses. This may be due to the fact that the primary concern of the fish during this period (the pre-nest period) is the establishment and maintenance of territory.

The total number of responses directed against the different dummies shows a distribution in the following way: $S_1 > S_4 > S_2 > S_3$, but the only significant difference appears to be between $S_1 > S_3$ (Wilcoxon's $T = 5$, $N = 10$, $p = .01$).

A significant difference between the dummies appeared in the number of aggressive responses when they were analysed separately from the non-aggressive responses (Table 1). Friedman's analysis of variance of these figures yields: $\chi^2_r = 9.39$, 3 df, $p < .05$. Paired comparisons revealed the following strong differences $S_1 > S_2$ (Wilcoxon: $T=6$, $N=10$, $p < .025$), $S_1 > S_3$ (Wilcoxon: $T=5$, $N=10$, $p < .01$) and between $S_1 > S_4$ (Sign-rank test: $x = 2$, $N = 10$, $p = .06$).

Table 1. Mean rank of the number of aggressive responses to the different stimuli ($N = 10$).

Stimulus	S_1	S_2	S_3	S_4
Mean	3.55	2.25	1.90	2.30

The specific results are further confirmed for aggressive responses when considering the number of periods with any aggressive response as the unit of measurement. The principal difference was $S_1 > S_3$ (Wilcoxon: $T=6$, $N=10$, $p < .025$), as could be expected from the earlier results. The distribution of this response measure over stimuli was similar to that of the frequency measure.

The trend is the same when the difference between aggressive and non-aggressive behavioural manifestations is con-

sidered, as well as when the difference between the number of periods with aggressive and the number of periods with any non-aggressive behaviour is calculated.

A difference between the dummies appeared very early during the habituation trials. Already after the first three half-minutes of testing a trend in the direction of $S_1 > S_4 > S_2 > S_3$ was evident (Friedman: $\chi^2_r = 7.13$, 3 df, $p < .10$).

Contrary to the 1971 results, however, no habituation over days was found, although habituation within each day's session was evident. This difference between the two studies may be due to the different number of presentations used.

In any case the result seems to indicate that the fish have directed the most frequent and intense attacks against the most structured stimulus (S_1). The stimulus which was attacked least seems to be S_3 which apart from S_4 is the stimulus with the lowest degree of structure. There are no significant differences to be found between the remaining stimuli but from the figures it can be concluded that the stimulus with least structure (S_4) received a great portion of the responses. This may be due to the fact that this stimulus is unitary grey. In a way it is the most fish-like stimulus. Thus the high number of responses could be due to past experiences of fish in general or to confusions with a female con-specific.

C o n c l u s i o n s

It seems hard to consider S_1 as possessing any signal-properties of the kind that Tinbergen suggests. Instead the outcome of the present experiment implies that some other quality of the stimulus situation affects the aggressive display. This other quality might be the degree of stimulation preceding and existing simultaneously with the specific attack (cf. Figler, 1972).

Since the sample used in this study is very small generalizations must be made with caution. It may however be appropriate to state the following hypotheses:

- (1) The prime function of the specific male colour pattern may be that of avoking female reproductive behaviour.
- (2) Regarding the territorial defence these specific hues may, as any highly structured stimulation, serve to orient the territory defending male towards intruders. Secondly the hues may attain the power to evoke territorial aggression through a process of conditioning -a process to which nest-raiding males (van den Assem, 1967) may contribute (cf. Wootton, 1970).

Further if the latter hypothesis proves to be correct we should also be provided with an explanation on a behavioural level of the earlier mentioned shift in aggressiveness between different phases of the male reproductive cycle.

R e f e r e n c e s

- Assem, J. van den- (1967). Territory in the three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour, suppl., 16, 1-164.
- Baerends, G.P. (1950). Specialization in organs and movements with a releasing function. Soc. exp. Biol., IV. Cambridge:Cambridge Univ. Press.
- Cohran, W.G. & Cox, G.M. (1957). Experimental designs. New York: Wiley.
- Figler, M.H. (1972). The relation between eliciting stimulus strength and habituation of the threat-display in male siamese fighting fish, *Betta splendens*. Behaviour, 44, 63-96.
- Hansson, S.B., Holmqvist, B. & Strömberg, I.B. (1971). Colour structures and extinction of aggressive display in the male three-spined stickleback (*Gasterosteus aculeatus* L.). Psychol. Res. Bull., Lund Univ., 11, No. 11.

- Hinde, R.A. (1966). Animal behaviour: A synthesis of ethology and comparative psychology. London: McGraw-Hill.
- Iersel, J.J.A. van (1953). An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L). Behaviour, suppl., 3, 1-159.
- Lehrman, D.S. (1953). A critique of Konrad Lorenz's theory of instinctive behaviour. Quart. Rev. Biol., 28, 337-363.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vögels. J. Ornith., 83, 137-213, 289-413.
- Lorenz, K. (1939). Vergleichende Verhaltensforschung. Verhandlungen der Deutschen Zoologischen Gesellschaft, Rostock. Zoologischer Anziegler, suppl., 12, 69-102.
- Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. Symp. Soc. exp. Biol., 4, 221-268.
- Lorenz, K. (1965). Evolution and modification of behaviour. Chicago: Univ. Chicago Press.
- Marler, P. (1961). The filtering of external stimuli during instinctive behaviour. In W.H. Thorpe & O.L. Zangwill (Eds), Current problems of animal behaviour. London: Cambridge Univ. Press.
- Muckensturm, B. (1968). La reaction des Epinoches aux leurres ne provient pas d'une confusion avec une congeneres. C.R. Acad. Sc. Paris, 266, 2114-2116.
- Peeke, H.V.S. Wyers, R.J. & Herz, M.J. (1969). Waning of the aggressive response to male models in the three-spined stickleback (*Gasterosteus aculeatus* L.). Anim. Behav., 17, 224-238.
- Peljwijk, J.J. ter & Tinbergen, N. (1937). Eine Reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus*. Zeitschr. Tierpsychol., 1, 193-201.
- Reventlow, I. (1970). Studier av komplicerade psykobiologiske faenomener. Copenhagen: Munksgaard.

- Schleidt, W. (1962). Die historische Entwicklung der Begriffe "Angeborenes Auslösende Schema" und "Angeborener Auslösmechanismus" in der Ethologie. Zeitschr. Tierpsychol., 19, 697-722.
- Seitz, A. (1940). Die Paarbildungen bei einigen Cichliden I. Zeitschr. Tierpsychol., 4, 40-84.
- Tinbergen, N. (1942). An objectivistic study of innate behaviour of animals. Bibl. Biotheor. Ser. D, 1, 37-98.
- Tinbergen, N. (1948). Social releasers and the experimental method required for their study. The Wilson Bull., 60, 6-51.
- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press.
- Tinbergen, N. (1952). The curious behavior of the stickleback. Sci. Am., 187, 22-26.
- Tinbergen, N. (1953). Social behaviour in animals. London: Methuen.
- Wootton, R.J. (1970). Aggression in the early phases of the reproductive cycle of the male three-spined stickleback (*Gasterosteus aculeatus*). Anim. Behav., 18, 740-746.

NOTES ON THE ETHOLOGICAL METHOD OF OBSERVATION

I. Selection of behavioural units

by

S. Birger Hansson

Lund, 1978

A b s t r a c t . - The author discusses the methodology of observation in relation to animal social behaviour with emphasis on the choice of behavioural units.

The following aspects are considered: (1) Intentional and unintentional selection. (2) The recording of events and states. (3) The status of the animal as actor and receiver.

The first section embraces a theoretical discussion. The following topics are illustrated with material obtained from personal observations of two samples of Cichlidae (*Pterophyllum scalare*).

A balanced intentional selection based on different but concordant operationally defined measures is recommended. Balance implies that an intentional selection does not work to reduce inclusiveness to artificial poverty.

I n t e n t i o n a l a n d u n i n t e n t i o n a l s e - l e c t i o n

An emphasis on pure (random, not goal-directed) observations as a basic methodological approach preceding any systematic analysis has always been characteristic of ethology (e.g. Lorenz, 1935 --- Blurton Jones, 1972). Such basic descriptions of the total behavioural repertoire of an animal are denoted "ethograms".

Once the ethogram is established subsequent work should proceed on four fundamental lines, i.e. causation, survival value, ontogeny and evolution (Tinbergen, 1963). The working rationale implies that the investigator influences to some extent (1) antecedent conditions of the behaviour and (2) the behaviour studied (Willems, 1969).

In the last case (2) the investigator makes an intentional selection of behavioural units from among the total array. This narrowing down of the data is done in accordance with the content of the hypothesis under consideration (Tinbergen, 1951).

Given that the array of behavioural acts is fairly extensive, it is reasonable to assume some kind of inverted relationship between the degree of intentional selection and the degree of unintentional selection (c.f. Arrington, 1939). The latter is dependent on the method applied and on observer characteristics. The erroneous influence of personal characteristics can be limited by using an index of inter-observer reliability and/or using a recording device such as video-tape or film. However, in the specific case of observations of animal behaviour this influence can be ruled out only to a limited extent. Since any observer has to go through a specially designed training period to get acquainted with the species, the impact of earlier experience always remains as does the governing effect of theoretical idiosyncrasy (Cooper et al., 1974 c.f. also Kaplan, 1964 p. 133). In the same manner the impact from the unique way of human perceiving cannot be eliminated (Klopfer, 1973 p. 18; c.f. also Lehrman, 1953). Consequently in dealing with behavioural studies on animals a claim of inclusiveness should balance against personal characteristics of the observer (c.f. Schneirla, 1950).

During observation certain movements of the animal are recorded. These are made part of the functional whole through an inductive analysis (based on analyses of the context and/or sequences of movements). The classification of behavioural units into concepts of a higher order (e.g. certain movements -- fighting behaviour -- aggression) is in essence arbitrary, however it is ideally balanced against careful descriptions which allow for detailed replications (Blurton Jones, 1972) and reconsiderations. The classification itself provides a basis for problem-centered observational studies (e.g. McGrew, 1972; c.f. also Tinbergen, 1951). Together with the problems which were posed the classification then constitutes a further aspect of intentional se-

lection. As such it also constitutes an influence on the answers to the problems.

Certain behavioural units cannot be classified unequivocally (Slater, 1973). Although they constitute part of the ongoing behaviour their informative value is low, since they do not in any decisive way add to the definition of a specific category.

Consider e.g. the discussion of spine-erection (spine-raising) in the three-spined stickleback. Van Iersel (1953) classified erection of dorsal spines as constituting part of fighting behaviour (a first sign of aggression), while he considered erection of pelvic spines as reflecting flight behaviour. In a detailed study on this topic Symons (1966) revealed a complicated relationship between spine-erection and certain other mutually inhibiting manifestations (zig-zaging and biting). Finally Wootton (1971) suggested that spine-erection (defined as simultaneous erection of both dorsal and ventral spines) reflects a reaction to novel stimulation.

Hypothetically, assuming that it is useful to make a differentiation between fighting behaviour and flight behaviour (thereby assuming that a study of aggression could be defined with reference to what is considered as fighting behaviour alone) the following suggestions could be appropriate:

- (1) Spine erection is a component of fighting behaviour (except when considering pelvic spines).
- (2) Spine erection is a component of flight behaviour (except when considering dorsal spines).
- (3) Spine erection reflects an ambivalent behaviour (conflict between fight and flight).
- (4) Spine erection reflects exploration behaviour (neither fighting- nor flight behaviour).
- (5) Spine erection reflects a general heightening of arousal level (neither fighting- nor flight behaviour).

Which behaviour unit will constitute part of a certain category is a matter of definition. However out of a claim of

universal comparability those behavioural acts which have a low informative value are questionable representatives of specific categories when appearing in isolation (c.f. Simpson, 1973a).

The recording of events and states
Event and state sampling based on different types of behaviour (case 1 and 2).

The behavioural stream can be analysed in terms of events and in terms of states (e.g. Simpson, 1973b). Behavioural acts considered at any single defining instant represent events and yield frequencies. States constitute durations and reflect percent of time spent in some activity (Altmann, 1974). Whether events or states are to be considered as suitable categories is dependent upon the specific questions initially posed. The two different approaches will measure different aspects of the same situation, and the existence of any specific relationship between these two aspects could not *a priori* be taken for granted (c.f. Dunbar, 1976).

On the other hand an interpretable relationship between these aspects may favour construct validity. Regarding social behaviour in animals Richards (1974) argues that a concept of dominance is useful as an explanatory device with some universal meaning only so far as it is based on different but concordant measures. An analysis based on data obtained both by event and state recording could be one way to fulfil this claim. As a case in point consider the following observations on social interaction in Cichlidae, species *Pterophyllum scalare*.

With reference to earlier research (Baerends and Baerends-van Roon, 1950) and personal observations, certain easily identifiable behavioural acts were selected and brought into one class of behaviour (which may be recognized as fight-

ing behaviour), namely: lateral display, tail-beating, frontal display, mouth fighting, butting and biting (for a description see Baerends et al., op. cit.). In the course of observations any representative of this class was considered as an event.

From earlier observations on this fish it was further suggested that differences in general locomotor activity reflect differences in rate of social interaction. Remembering that the fish eye seems especially designed to detect movements (Ingle, 1971) any duration of a movement (equal to and more than 1 sec.) was considered a state (movement: a transfer in space).

Finally it was assumed that these measures were interrelated, and that recording by means of events or states would yield comparable data.

Method.

Eleven specimen of *Pterophyllum scalare* (Pisces: Cichlidae) were observed in a well-planted and evenly illuminated 160 l aquarium. Fish had been bought from a local dealer and kept under constant conditions for approximately 2 months. Observations were systematised in accordance with techniques of time-sampling (not implying any one-zero sampling) and focal animal sampling (for further discussion on focal animal sampling see Altmann, 1974; Hansson, 1978).

For consecutive periods of 9 and 8 days respectively three sessions of observation were spread over each day. Within each session one animal was initially selected as focal and observed for 5 minutes, after which another animal was selected and observed for the same amount of time. After a pause of 5 minutes the procedure was repeated with new focal animals until every fish had become focal. The selection of focal animals was systematized to avoid sampling errors.

Case 1 - event sampling: Fish were observed for a period of 9 days. The recording was performed with the help of an event-recorder. Case 2 - state recording: Fish were observed for a period of 8 days. The study was performed a week after Case 1 on the same fish.

Analysis of results.

The distribution of behavioural acts that each fish produced in Case 1 is revealed in Table 1. Individual sums over days were transformed into ranks to denote relative positions between fish.

Table 1. Ranking of fish according to behavioural acts produced over days obtained by event recording (highest rank reflects greatest magnitude).

Fish	A	B	C	D	E	F	G	H	J	K	L
Ranks	10	11	8	5	3	1	4	7	2	6	4

Case 2 - state recording - yielded a dispersion between fish with regard to the total time of locomotion over days. This is shown in Table 2.

Table 2. Dispersion between fish regarding duration of locomotor activity summed over days (Friedman: χ_r^2 : 49.57; $p < .001$).

Fish	A	B	C	D	E	F
Sum of ranks	70.5	74.5	64.0	41.0	14.0	36.0
cont.						
Fish	G	H	J	K	L	
Sum of ranks	38.0	56.0	15.0	55.0	64.0	

The stability of locomotion over all sessions for individual fish was further analyzed. Variances were transformed to ranks to denote relative positions between fish in this respect. When compared with ranks in Table 2 a correlation of $r_s = -.80$ was revealed. Thus high-responsive fish tend to be stable in respect to variations in locomotor activity, while low-responsive fish tend to be unstable.

Finally the results revealed in Table 1 (Case 1) and Table 2 (Case 2) were compared with each other. This yielded a correlation where $r_s: +.88$. Great variation with respect to locomotion in low-responsive fish probably depends on their keeping away from high-responsive fish.

It was concluded that both measures (frequency of behavioural acts and general locomotor activity) obtained by different recording techniques could be used to describe the same social reality.

Event and state sampling based on the same type of behaviour (Case 3 and 4).

In connection with the observations recorded in Case 2, further notations were made during five days of frequencies of events (like in Case 1). Since the event recorder mentioned in connection with Case 1 yielded information not only of frequencies of events but also on the duration of events, it became possible to compare the results of observations based on frequencies with those based on seconds in both Cases, that is to take into account the length of each display as well.

As will be recalled each period of observation lasted for five minutes (300 sec.). Since the number of frequencies produced never exceeded 300 in any period of observation, it became feasible to consider one event as constituting one second. Thus the number of events and durations could be measured on the same scale (number of seconds).

Thus we are left with three measures:

- (1) A total time score that is the total duration of different fighting activities during a 300 sec. session (here denoted T).
- (2) The frequency of events measured in seconds, where one event was equivalent with one second (N).
- (3) A measure of fighting activity independent of the frequencies (N), which is the length of the displays minus one second for each display (T-N).

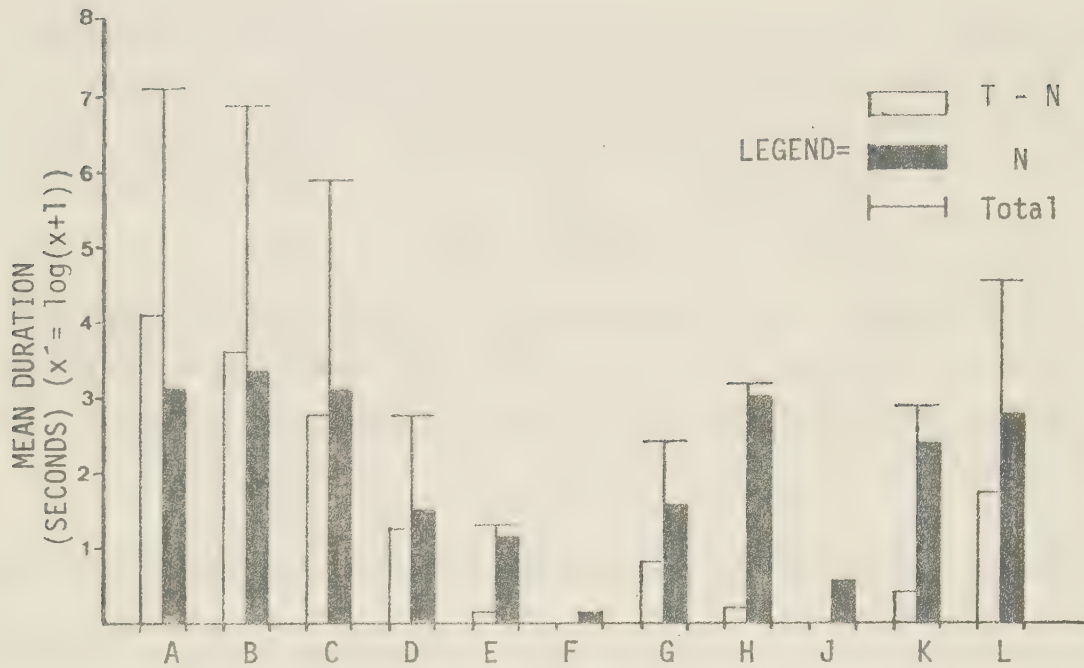


Fig. 1. Mean magnitude of individual activity (Case 3).

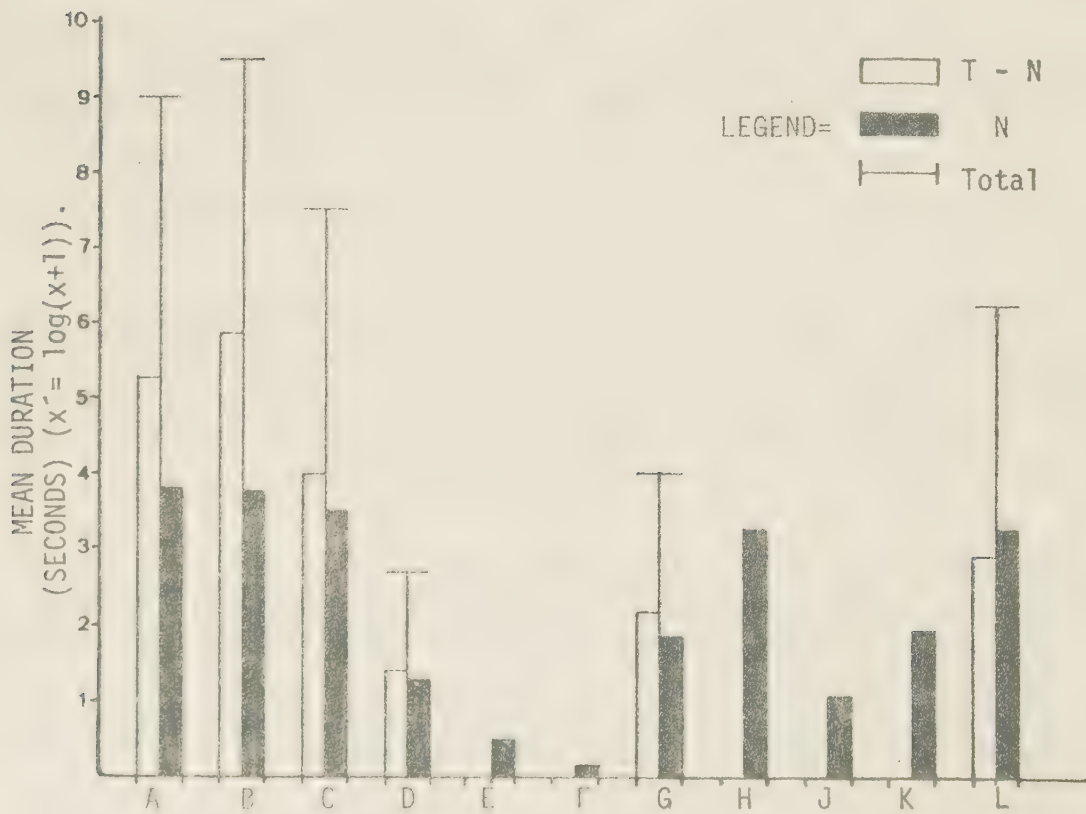


Fig. 2. Mean magnitude of individual activity (Case 4).

Internal sample characteristics.

Measures on fighting activity independent of the frequencies (T-N) of each Case were treated by means of analysis of variance with Days and Subjects as main factors. In order to stabilize the variances (Winer, 1970, p. 221) the time scale (number of seconds) was transformed into a logarithmic scale where $x' = \log(x+1)$. The resulting distributions can be seen in Fig. 1 (Case 3) and Fig. 2 (Case 4).

It will be recalled that there had been three sessions of observations each day, therefore before applying the analysis of variance it was necessary to find out if any systematic variance between sessions was manifest. Data were treated by Friedman's two-way analysis of variance and the results were found to be non-significant (Table 3). Thus it could be concluded that there was no pronounced systematic variance between sessions attributable to e.g. daily rhythms etc.

It is shown in Table 4 that the analyses of variance show differences between Days as well as between Individuals in both Cases. Further the analyses yielded significant interactions.

Thus the amount of display obviously differentiates between high- and low active days and individuals as well as it yields information about individual activity profiles over days.

Table 3. Variance between sessions of observations.

Sessions of observation		First	Second	Third
Mean rank	Case 3	2.11	2.11	1.78
	Case 4	2.20	1.60	2.20

$\chi^2_{r \text{ Case 3}} : .558; N 9.$ $\chi^2_{r \text{ Case 4}} : 1.200; N 5.$

Table 4. Results of analysis of variance on data (T-N) from Case 3 and 4 with Days and Subjects as main factors.

Sample	Case 3	Case 4
Days	$p < .01$	$p < .01$
Subjects	$p < .01$	$p < .01$
Days $\times$ Subjects	$p < .01$	$p < .05$

To grasp the meaning of this measure it is however necessary to see it in relation to the frequencies of events (N). Correlations between N and T-N (based on log.scale) yield in Case 3 $r = .71$, $df\ 9$, $p < .05$ and in Case 4 $r = .78$, $df\ 9$, $p < .01$ (correlations based on seconds yield approximately the same results). Thus those fish which manifest long displays also manifest high frequencies of events. This conclusion is further confirmed by rank correlations between the total time score (T) and N where $r_{s_{Case\ 3}} = .95$, $N\ 11$, $p < .01$ and $r_{s_{Case\ 4}} = .98$, $N = 11$, $p < .01$ (rank correlations based on seconds).

However an inspection of Figs 1 and 2 reveals that despite the apparently high association between N and T-N there exist important deviations. In both Case 3 and 4 fish H manifests a high frequency of events but short durations. Even though it could be argued the fish H obviously played a special role in the group (which will be commented on in a later study, Hansson, 1978), it may nevertheless be that conclusions based on the duration of display do not cover all relevant aspects of the social behaviour in the aquarium.

Between sample characteristics.

A significant positive relation was found between Case 3 and Case 4 when the individual duration of display was considered as a proportion of the individual total where $r = .95$, $df\ 9$, $p < .01$ (correlation based on seconds; when

based on log. scale: $r = .98$). Further a similar result was obtained when the individual duration of display was considered as a proportion of the respective sample total, $r = .95$, respective $r = .98$.

Thus the individual durations appear to be consistent and those individuals manifesting long displays in Case 3 do so in Case 4 as well.

Figs 1 and 2 yield the impression of differences between Case 3 and 4 when regarding level of responsiveness. No such differences were however to be found when considering T-N as proportions. On the other hand when regarding individual means based on the total number of seconds (log. scale) in respective samples a difference appears between durations (T-N) where $t = -2.31$, $df\ 10$, $p < .05$.

Thus the displays in Case 4 seem over all to be longer than in Case 3. Figs 1 and 2 reveal that this increase in display activity could be attributed to the high frequency fish.

Conclusions.

An analysis based on events or durations will lead to statistically the same conclusions. However an analysis based on frequencies of events seems to more inclusive than that based on durations.

Both measures appear to be consistent. A trend towards high active fish becoming more active and low active fish less active with time spent together in the aquarium appears first to be seen in length of display.

The animal as actor and receiver
(Case 5 and 6)

Dealing with the recording of events within the frame of

focal animal sampling we may obtain two categories of records: (1) Behavioural acts produced by an animal reflecting the state of the animal as actor in the society. (2) Behavioural acts produced against an animal reflecting its state as a receiver (Altmann, 1974).

The relationship between these categories presumably fluctuates with the particular focus of study and with the measures decided upon. Dealing with behaviour in groups there is no reason to assume *a priori* the existence of any linear relationship. Considering the animal not only as actor but as a receiver as well may yield a more sensitive definition of its part in the social interaction. The following study represents an illustrative case on this point.

Method.

Case 5 - a society during establishment (during establishment, as compared to established in a relative sense). Six specimen of *Pterophyllum scalare* (Pisces: Cichlidae) were observed in a well-planted and evenly illuminated 100 l aquarium. The fish had been bought from a local dealer and observations started 3 days after they had been let into the aquarium.

Case 6 - an established society. Eleven specimen were observed under the above conditions but in a 160 l aquarium. Observations started approximately six weeks after the fish had been let into the tank.

In both cases the fish were observed during nine consecutive days. As before (Case 1 - 4) observations were systematised in accordance with techniques of focal animal sampling and time sampling. In Case 5 every animal became focal four times a day, in Case 6 three times a day at intervals during the day (yielding total times of observation of 20 and 15 minutes a day respectively). The order of focal animals was systematised to avoid sampling errors. Behavioural acts defined in connection with Case 1 were recorded by means of a mechanical event recorder (a modified two-channel writer).

The data were treated by means of analysis of variance (Wiener, 1970, p. 162), where the following factors are relevant for the discussion: behavioural acts produced and received (Categories), their interaction with subject records (Sub-

jects) and with day records (Days). In addition differences between sessions were considered. This factor may reflect inconsistency of behaviour (the question of daily rhythms has been treated above).

Analyses of results.

Case 5 - a society during establishment.

The data reflect no difference between the total number of behavioural acts produced and received (Categories) (Table 5).

Table 5. The main effect (Categories) and its interaction with the factors Days and Subjects.

Source of variance	MS	F	P
Between Categories	.11	.003	>.05
Categories × Subjects	318.89	8.81	<.01
Categories × Days	7.33	.02	>.05
Categories × Subjects × Days	70.12	1.94	<.01
Between sessions	36.18		

It is, on the other hand, evident from Table 5 that Categories interact with Subjects. A graphic representation of this interaction (Fig. 3) reveals that among the fish subject γ^x produced few behavioural acts but received many, while the reverse applies to subject ϵ .

As is indicated in Fig. 3 paired comparisons over sessions confirm the stability of differences between the two categories in the case of subject γ ($p < .001$; t : 4.533, df 35) as well as in the case of subject ϵ ($p < .001$; t : 5.635; df 35).

^x The greek letters represent individual fishes - not their place in a ranking order.

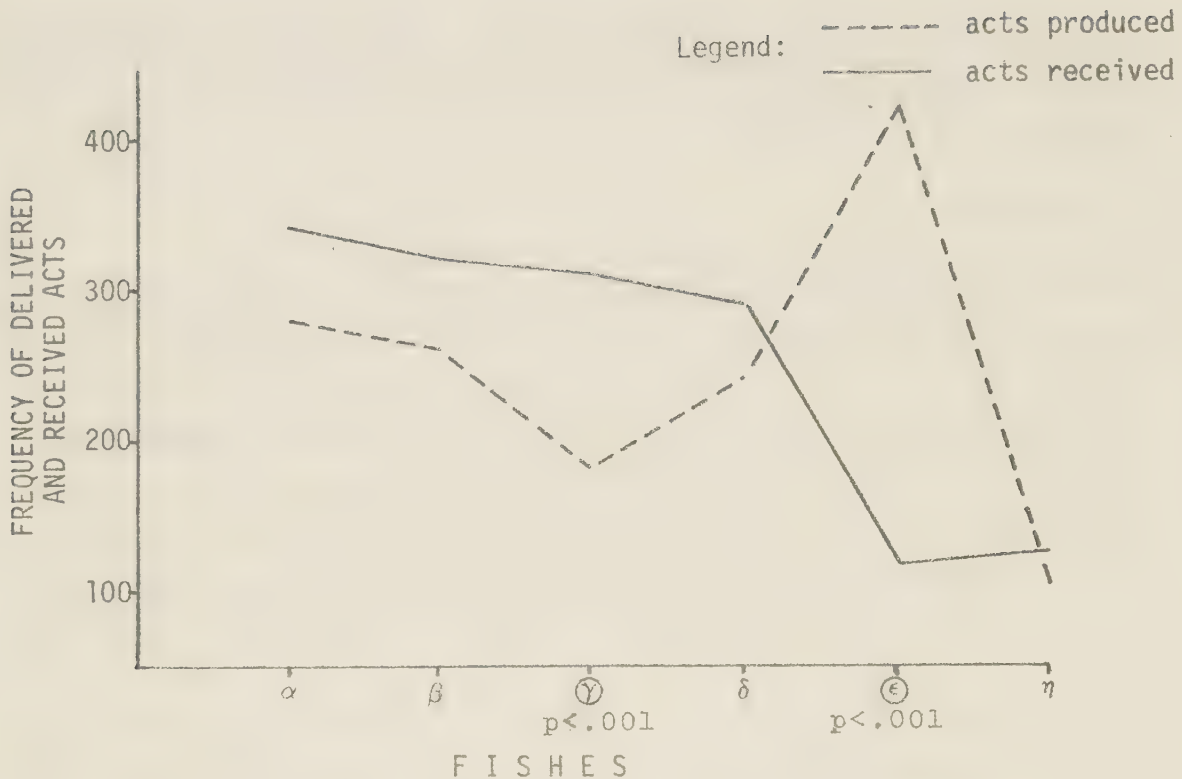


Fig 3. The interaction Subjects $\times$ Categories (acts produced vs. received) (Case 5).

Within this miniature society fish evidently exhibit four styles of adaptation: (1) High frequency of production vs. low frequency of reception. (2) Production and reception of a statistically equal amount but on a fairly high level of frequency. (3) Low frequency of production vs. fairly high frequency of reception. (4) Production and reception of a statistically equal amount but on a low level of frequency. It is evident from Table 5 that apart from individual differences the distribution of behavioural acts over categories is stable over days ($r: +.90$).

Finally the data reflect a three-factor interaction (Categories $\times$ Subjects $\times$ Days) where $p < .01$ (Table 5). Apparently certain fish change their style of adaptation over days. Such a shift is evident in the case of subjects β and γ .

The phenomenon probably depends on hormonal fluctuations (as will be discussed later, Hansson, 1978).

Case 6 - an established society. The data reflect no difference between the total number of behavioural acts produced and received (Categories) (Table 6).

Table 6. The main effect (Categories) and its interaction with the factors Days and Subjects.

Source of variance	MS	F	P
Between categories	2.19	.009	>.05
Categories × Subjects	317.95	14.98	<.001
Categories × Days	13.82	.56	>.05
Categories × Subjects × Days	28.45	1.15	>.05
Between sessions	24.77		

On the other hand it is revealed that Categories interact with Subjects. The graphic representation of this interaction (Fig. 4) shows that fish B and H have produced many but received proportionally few behavioural acts. Paired comparisons confirm the stability of these differences over sessions in the case of fish B: $p < .001$ (t : 7.529; df 26) and in the case of fish H: $p < .001$ (t : 8.865).

The data also reflect the reverse condition. It is evident from Fig. 4 that fish J and D have received many behavioural acts while producing few. In the case of fish J a difference between categories is revealed ($p < .001$; t : 4.653) as it is in the case of D ($p < .001$; t : 4.752). The same trend is also evident in the case of fish F ($p < .01$; t : 3.172).

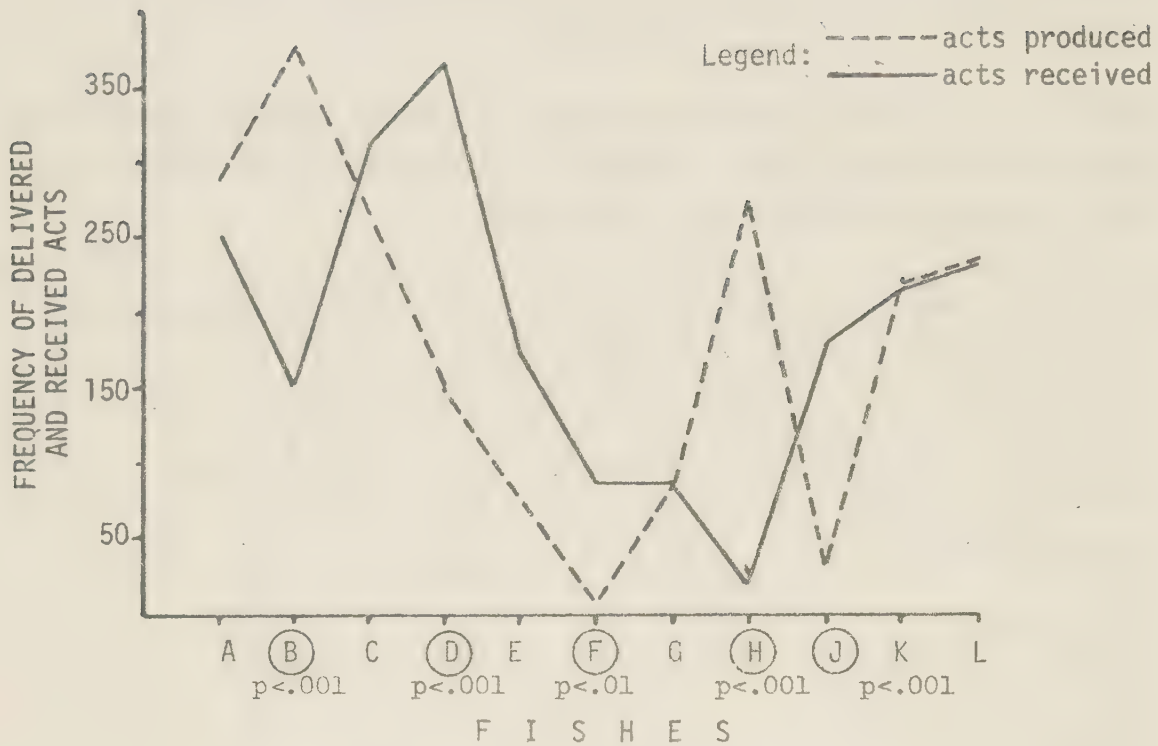


Fig. 4. The interaction Subjects $\times$ Categories (acts produced vs received) (Case 6).

Consequently the members of this miniature society present diverse styles of adaptation. The following tendencies are conspicuous: (1) High frequency of production vs. low frequency of reception. (2) Low frequency of production vs. high frequency of reception. (3) Production and reception of a statistically equal amount but on a fairly high level of frequency. (4) Production and reception on a low level of frequency. These data support those found in Case 5.

Within this group the distribution of behavioural acts produced and received remained in all respects stable over days, since neither category was found to interact with days, nor did the data support the presence of any three-factor interaction (Categories $\times$ Subjects $\times$ Days) (Table 6). Presumably hormonal fluctuations do not affect interaction

within a proportionally established society to the same extent as in a society during establishment.

Consequently if a level of analysis is chosen which demands a detailed description of the social intercourse both social acting and receiving should be considered as relevant factors.

G e n e r a l d i s c u s s i o n

In dealing with observations of social behaviour in animals data-selection is affected by the uni-directional character of the task, by the complexity of the stimulus-situation and by personal characteristics of the observer. A balanced intentional selection based on different but concordant operationally defined measures, offers manageable structure as well as replication. The claim of balance implies that selection does not reduce inclusiveness to artificial poverty.

R e f e r e n c e s

- Altmann, J. (1974) Observational study of behaviour:sampling methods. Behaviour 49, 227-267.
- Arrington, R.E. (1939). Time-sampling studies of child behaviour. Psychol. Monogr., 51.
- Baerends, G.P. & Baerends - van Roon, J.M. (1950). An introduction to the study of the ethology of cichlid fishes. Behaviour, suppl., 1, 1-242.
- Blurton Jones, N. (1972). Characteristics of ethological studies on human behaviour. In N. Blurton Jones (Ed.), Ethological studies of the child. Cambridge: Cambridge Univ. Press.
- Cooper, E.S., Costello, A.J., Douglas, J.W.B., Ingleby, J.D. & Turner, R.K. (1974). Direct observation? Bull.Br.psy-chol. Soc., 27, 3-7.
- Dunbar, R.I.M. (1976). Some aspects of research design and their implications in the observational study of behaviour. Behaviour, 58, 78-98.

- Hansson, S.B. (1978). Notes on the ethological method of observation. II. Focal animal sampling. Mimeo, Lund University, Sweden.
- Iersel, J.J.A. van (1953). An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour, suppl., 3, 1-159.
- Ingle, D. (1971). Vision: The experimental analysis of visual behaviour. In W.S. Hoar & D.J. Randall (Eds), Fish physiology, V. London: Academic Press.
- Kaplan, A. (1964). The conduct of inquiry. Methodology for behavioural science. Pennsylvania: Chandler Publ. Co.
- Klopfer, P.H. (1973). Behavioural aspects of ecology. London: Prentice Hall.
- Lehrman, D.S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. Quart. Rev. Biol., 28, 337-363.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. J. Ornithol., 80, 137-312, 289-413.
- McGrew, W.C. (1972). An ethological study of children's behavior. New York: Academic Press.
- Richards, S.M. (1974). The concept of dominance and methods of assesment. Anim. Behav., 22, 914-930.
- Schneirla, T.C. (1950) The relationship between observation and experimentation in the field study of behavior. Ann. N.Y. Acad. Sciences, 51, 1022-1044.
- Simpson, M.J.A. (1973a). Social display and the recognition of individuals. In P.P.G. Bateson & P.H. Klopfer (Eds), Perspectives in ethology. London: Plenum Press.
- Simpson, M.J.A. (1973b). The social grooming of male chimpanzees. In R.P. Michael & J.H. Crook (Eds), Comparative ecology and behaviour of primates. London: Academic Press.
- Slater, P.J.B. (1973). Describing sequences of behaviour. In P.P.G. Bateson & P.H. Klopfer (Eds), Perspectives in ethology. London: Plenum Press.
- Symons, P.E.K. (1966). Analysis of spine-raising in the male three-spined stickleback. Behaviour, 26, 1-75.

- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press.
- Tinbergen, N. (1963). On aims and methods of ethology. Zeitschr. Tierpsychol., 20, 410-433.
- Willems, E.P. (1969). Planning a rationale for naturalistic research. In E.P. Willems & H.L. Raush (Eds), Naturalistic viewpoints in psychological research. New York: Holt, Rinehart & Winston.
- Winer, B.J. (1970). Statistical principles in experimental design. London: McGraw-Hill.
- Wootton, R.J. (1971). Measures of the aggression of parental male three-spined sticklebacks. Behaviour, 40, 228-262.

NOTES ON THE ETHOLOGICAL METHOD OF OBSERVATION

II. Focal animal sampling

by

S. Birger Hansson

Lund, 1978

A b s t r a c t . - The author discusses the methodology of observation in relation to animal social behaviour with emphasis on sampling techniques.

Focal animal sampling was applied to three cases of group behaviour in an aquarium (a group during establishment -N=6, an established group -N=11 and a replica of the latter case -N=11) by *Pterophyllum scalare*.

The primary goal of the study was to obtain some idea of the reliability of the focal method. The secondary goal was to reveal the existence of any group structure within the samples.

The reliability was found to be high. Within the males the group structure could be described as a branching dominance hierarchy, with the females interaction was mainly found to be pairwise.

I n t r o d u c t i o n

The social behaviour of a subhuman animal is a product of a functional whole which is in essence unknown to the human observer. The significance of any single behavioural act must be inferred from the totality, specific and general ecological demands, behavioural context, species characteristics and the physiological status of the actors under consideration. To prescribe the animal's place in this whole is a matter of interpretation.

Although the human observer is aware of the fact that animals perceive in a unique way, it is handy, and sometimes inevitable, to describe behaviour within a human conceptual frame of mind (Lorenz, 1935). The outcome is often a mixture between a behaviouristic and phenomenological data-language (Christiansen, 1975). Interpretations penetrate the descriptive level.

In addition, when observing certain aspects of non-verbal social behaviour, the observer no longer remains just an observer but becomes an active recipient of those signals which he intends to record and describe in an objective way. This may affect both the data-language and the data-selection.

It is a truism that in any observational study dealing with non-verbal social behaviour, our way of receiving and selecting, of describing and interpreting information is a source of influence. Evolution has provided the human observer with a nervous system different from that of any other species, consequently studies on subjects belonging to a phyletic level different from our own are particularly susceptible to these influences (c.f. Lehrman, 1953). Thus, it seems important that the stimulating naturalness of the inductive ethological approach become associated with an increased methodological sophistication in the collection of data.

The aquarium as a miniature situation

The naturalness of a research situation is limited by the experimenter imposing conditions on the animals (Willems, 1969; Hansson, 1978). As regards the aquarium situation, animals are more or less forced together and are forced to live in a more or less restricted area. Consequently, the aquarium situation is generally considered to be semi-natural (e.g. Box, 1973).

There are then two aspects of the utility of the aquarium for observations of social behaviour, one applies to method and the other to behaviour:

(1) The aquarium is useful as a miniature situation when developing and testing methods of observation.

The aquarium offers a controllable replica of nature. Ecological complexity as well as social complexity (including rate of occurrence) are variable factors. Specific ecological and social conditions may be arranged. Observations may be carried out at any hour of the day. Any suitable design and sampling method may be applied.

(2) The aquarium is of restricted utility when investigating processes of social behaviour.

However well-equipped for the specific demands of a species, an aquarium is nevertheless an artificial world. This may promote the occurrence of behaviour that is qualitatively or quantitatively different from that which normally appears in nature (cf. Lorenz, 1965). Unless very large tanks are used no direct generalisations can be drawn from a behaviour manifested in the aquarium to what should be considered an event in nature. (Consider i.e. that overcrowding may evoke a transition from normal pair formation to the establishment of dominance relations, Wilson, 1975; that enclosure hinders normal migratory behaviour and may give rise to fluttering - swimming up and down against the glass-wall, van Iersel, 1953).

T h e o b s e r v e r a s a v a r i a b l e

The occurrence of relatively quick adaptation to the presence of an observer has been reported for humans (e.g. McGrew, 1972), and it seems reasonable to suggest that this may also apply to captive animals. There is however, a difference in kind between observer influence on the social behaviour of humans and animals. Theoretically for animals humans should represent on one hand a regular supply of food and on the other hand a potential threat. Since most animals are extremely sensitive to movements, an adaptation which they have acquired could easily be destroyed by the slightest incautious movements by the human observer. The relative import of this potential influence should presumably be selective on qualitatively different aspects of the behavioural stream, and therefore, especially when manifest to a low degree, constitute a source of bias which is hard to control. To a certain extent this potential influence could be lessened by using screens. A disadvantage, however, is that screens could impair observational accuracy by reducing the momentary visual field. Further video-tape presents a two-dimensional representation of a three-dimensional reality which can be hard to interpret (Cooper et al., 1974).

B e h a v i o u r s a m p l i n g t e c h n i q u e

Different strategies have been used in order to reduce biased sampling in observational studies of social behaviour. In

a review of the major types of techniques available in ethological literature Altmann (1974) argues that in order to choose a sampling technique the observer needs to consider carefully the characteristics of behaviour and social interactions that are relevant to the population being studied and the research questions at hand. It is often possible to combine techniques either successively or concurrently (e. g. Abramovitch, 1976).

Four different sampling techniques of interest for the following discussion and commonly used in ethology are briefly discussed below. The headings correspond with those earlier used by Altmann, op.cit.

Ad libitum sampling. This strategy is unsystematic and random. Observations are made without reference to defined rules for selection of animals and behavioural acts. The approach may be of heuristic value and could be applied in connection with pilot studies in the early phase of a new project (cf. Menzel, 1969).

Sampling all occurrences of some behaviour. During each defined observation session all occurrences of a class of behaviours in all members of a group are recorded. The advantage of this strategy lies in the opportunity to obtain high-synchronisation of data since continuity and context are considered. The disadvantage is that it demands high attention by the observer, excellent observational conditions and behavioural acts that do not occur too frequently. Consequently with this method there is great risk of obtaining a lot of influence from unintentional selection (Altmann, op.cit.; Hansson, 1978; cf. also Simpson and Simpson, 1977).

Sampling sequences of behaviour. The sampling is based on interaction sequences. A sample period begins when an interaction begins. All behaviours under study are recorded in order of occurrence. The primary difficulty with this method stems from the problem of selecting sequences and identifying their beginning and end (Altmann, op.cit; cf. Newston and Enquist, 1976).

Focal animal sampling. The technique implies a sampling accomplished on the basis of individuals and aims at making a complex stimulus field more accessible to the observer. During a specified period of time every occurrence of a specified action or interaction of an individual or a group of individuals is recorded. The strategy implies that focal animals are chosen in a systematic way (or with sufficient sample size, at random) (Altmann, op.cit.).

Since total behaviour is recorded in sequences, the increase in reliability which may be obtained by this method could be accompanied by decreased validity, since records obtained will lack continuity and adequate context (Arrington, 1943; cf. also Hansson, 1978).

In the case of observational studies on group behaviour the focal method is often the method chosen (Altmann, op.cit). It is suggested that this method is most appropriate when applied to studies intended to reveal structural properties within groups or between groups, thus it seems most suited for descriptive studies of group behaviour. When aiming at analyzing sequences of behaviour each focal period should be assigned sufficient time to permit such an analysis. Further since the focal method is not well-suited for studies on synchronization of behaviour, its value in studies on causality may be impaired.

The focal method applied

The focal method has earlier been applied to observations of the behaviour of fish under natural conditions by Wootton (1972). The present study aims primarily at an assessment of the method by applying it to observations of the social interaction of fish kept in an aquarium. A subsidiary goal is to reveal the existence of social structure in the groups observed.

The concept of dominance.

The actual behaviours used by observers to judge dominance are as diverse as the species studied (Brown, 1975). Frequently dominance is judged on the basis of aggression (aggressive orders) or of competition (competitive orders) (Syme, 1974), but measures such as mounting, grooming and play have also been used (Wilson, 1975). It has been argued (Richards, 1974) that if a concept of dominance is to be useful, independent measures should be chosen which cut through many commonly occurring situations. If these measures, are shown to correlate then the concept could be retained. Difficulties in obtaining such an external validity have led to questioning of the classically postulated unidimensionality of the concept (Syme, op. cit.).

Further, within animal psychology a distinction is traditionally made between despotism, peck-right hierarchies and peck-dominance hierarchies^x. Among these the peck-right hierarchy represents the case of a true hierarchy, since the relation "is superior to" is transitive throughout (and always is). The case of despotism (although in the same manner a true hierarchy) is uninteresting because of its shallowness. Finally, the peck-dominance, which is characterised by occasional reversals, could only in a limited sense be considered a true hierarchy (Dawkins, 1976; Masure and Allee, 1934; cf. also Baerends and Baerends-van Roon, 1950).

Like territory, dominance is irregularly distributed throughout the animal kingdom (Wilson, 1975). In fact the existence of hierarchies (mostly peck-/nip-/dominance) has been demonstrated for several species of fish in the laboratory, in a few cases also in the field (see Myrberg, 1972 and Jenkins, 1969 for reviews). The idea of individual recognition is an important aspect of the phenomenon of dominance. This capacity has been documented in at least some species of teleosts (Zayan, 1974, 1975). Further some kinds of fish have been reported to show an easy transition between territorial defense and dominance orders (e.g. Greenberg, 1947; Erickson, 1967; discussion in Wilson, 1975).

M e t h o d

Case I - a society during establishment (Frey and Miller, 1972) (during establishment as compared to established in a relative sense). Six specimen of *Pterophyllum scalare* (Pisces: Cichlidae) were observed in a well-planted and evenly illuminated 100 l aquarium. The fish had been bought from a local dealer and observations started 3 days after they had been let into the aquarium.

Case II - an established society. Eleven specimen were observed under the above conditions but in a 160 l aquarium. Observations started six weeks after the fish had been let into the aquarium.

Case II was replicated a week after the completion of the original study (the original study is denoted Case IIa the replica Case IIb).

In Case I and Case II fish were observed during nine consecutive days, in Case IIb during five consecutive days. Observations were systematized in accordance with focal animal sampling and time-sampling techniques (time-sampling in its literal sense and thereby not implying any one-zero sampling). In Case I four sessions of observations were spread over

^x The usefulness of the distinction between peck-right and peck-dominance hierarchies has lately been questioned (Brown, 1975). A categorisation dependent on site-dependency vs. -independency has been suggested instead. Here peck-right/-dominance is used in accordance with Myrberg, 1972).

each day. Within each session one animal was initially selected as focal and observed for five minutes, after which another animal was selected and observed for the same time. After a pause of 5 minutes the procedure was repeated with new focal animals until each fish had become focal. In Case IIa and Case IIb the same procedure was adopted except that each animal was observed three times each day. In both cases the selection of focal animals was systematised to avoid sampling errors.

Behavioural acts were recorded by means of a two-channel event recorder. In this way the behaviour of the animal both when receiving and producing behavioural acts could be recorded (Altmann, 1974; see also Hansson, 1978 where the relation between producing and receiving has been discussed in detail).

The nature and direction of behaviours produced and received was simultaneously recorded by means of a tape recorder. Due to technical difficulties the data from Case I could however not be analysed in this respect.

The following behavioural acts were recorded: lateral display, tail-beating, frontal display, mouth fighting, butting and biting. These were considered as representing fighting behaviour. (Baerends et al., 1950). In the course of the observations any representative of fighting behaviour thus defined was considered an event (Altmann, 1974; Hansson, 1978 for the relation between events and durations).

A n a l y s i s o f r e s u l t s

Data were treated in two ways:

(1) Quantitative analysis: Frequencies of behavioural acts were considered with respect to differences between the main variables: Individuals, Days and Categories (acts produced vs. received). Further interactions between these variables were considered.

(2) Qualitative analysis: Frequencies of behavioural acts were considered to reveal the direction of individual choices. This analysis could only be performed on data from Case IIa and IIb.

(1) Quantitative analysis.

Main effects.

Within each Case differences were revealed with regard to the distribution of the total number of behavioural acts between days (Table 1). Thus the number of recorded acts did not remain constant from day to day.

Table 1. Analysis of variance on data from Case I, IIa and IIb.

	Case I	Case IIa	Case IIb
Source of variance	p	p	p
Between days	<.01	<.01	<.01
" subjects	<.01	<.01	<.01
" categories	>.05	>.05	>.05
Days × subjects	<.01	<.01	<.01
Days × categories	>.05	>.05	>.05
Subjects × categories	<.01	<.01	<.01
Days × subjects × categories	<.01	>.05	>.05
Within sessions (MS)	41.39	24.77	31.70

It was further found that the number of behavioural acts in all Cases varied among group members (Table 1). Certain fish contributed more than others to the totality of observed behavioural acts.

The variation between individuals within the three Cases is revealed in Table 2. Most interesting here is the agreement between Case IIa and IIb. The correlations obtained are highly significant, but it should be observed that there are small changes. Thus in terms of level of frequencies the order between individuals is somewhat changed from Case IIa to IIb.

Table 2. Distribution of behavioural acts between individuals within Case I, IIa and IIb. Means of acts produced and received.

Acts produced.

Case I	Subject	α	β	γ	δ	ϵ	η					
	Mean	10.44	9.70	6.70	8.96	15.33	3.70					
Case II	Subject	A	B	C	D	E	F	G	H	J	K	L
	a Mean	10.4	13.9	10.3	5.6	2.7	.3	3.3	10.1	1.2	8.9	10.6
	b Mean	19.5	18.5	16.1	4.9	.6	.3	5.5	13.1	2.3	4.5	12.8

$r_{s \text{ IIa/IIb}}$: .91, $N=11$, $p<.01$

Acts received.

Case I	Subject	α	β	γ	δ	ϵ	η					
	Mean	12.70	12.00	11.56	9.89	4.30	4.67					
Case II	Subject	A	B	C	D	E	F	G	H	J	K	L
	a Mean	9.5	5.6	11.6	13.6	6.4	3.3	3.3	.7	6.5	8.8	9.7
	b Mean	16.7	14.2	10.2	12.6	3.4	4.5	6.7	.6	8.9	7.6	9.9

r_s IIa/IIb: .67, $N=11$, $p<.01$.

The number of frequencies was found to be equally distributed between the two categories in all Cases.

Interactions.

Although differences between days were found to be unequally pronounced within the categories (when considered separately) of Case I and IIa, these differences did not manifest themselves in any strong interaction pertaining to the three-factor analysis.

The distribution of behavioural acts between individuals was however found to interact with categories in all Cases (Table 1), thus some fish did not produce and receive acts in an equal way. This phenomenon has been commented on in an earlier report of this series (Hansson, 1978) and was then interpreted in terms of individual style of adaptation to ongoing social reality.

Days $\times$ Individuals - Case I: Interactions between individuals and days were found in all Cases. Regarding Case I the interaction was further evident when acts produced were considered separately ($p<.01$). The difference between categories in this respect also manifested itself in an interaction of higher order (Days $\times$ Individuals $\times$ Categories) (Table 1).

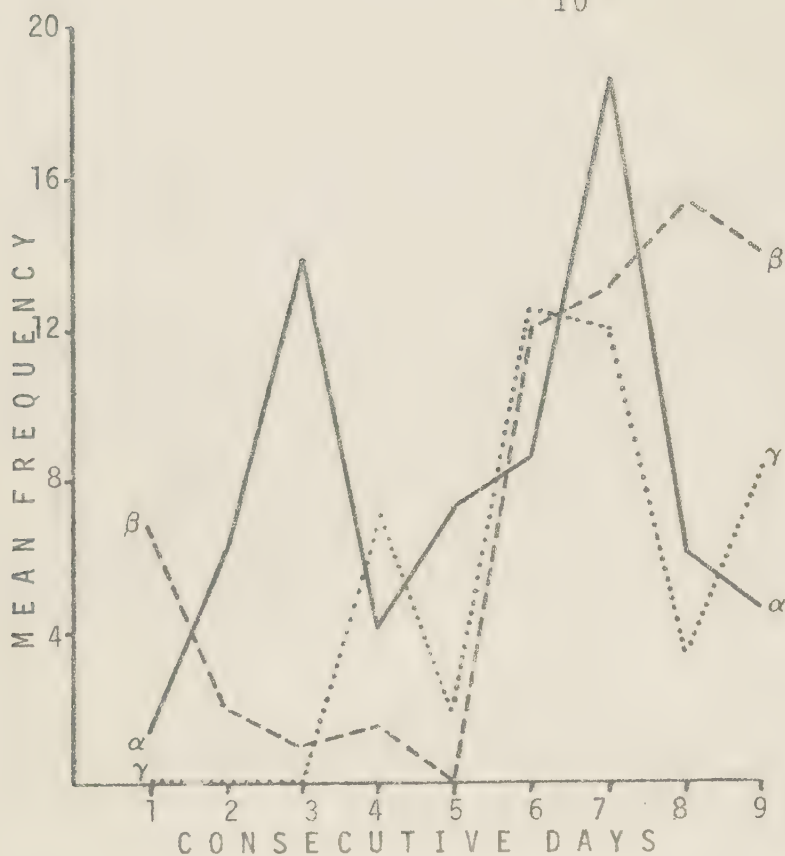


Fig. 1. Graphic representation of the distribution of responses over days (means) within Case I (females).

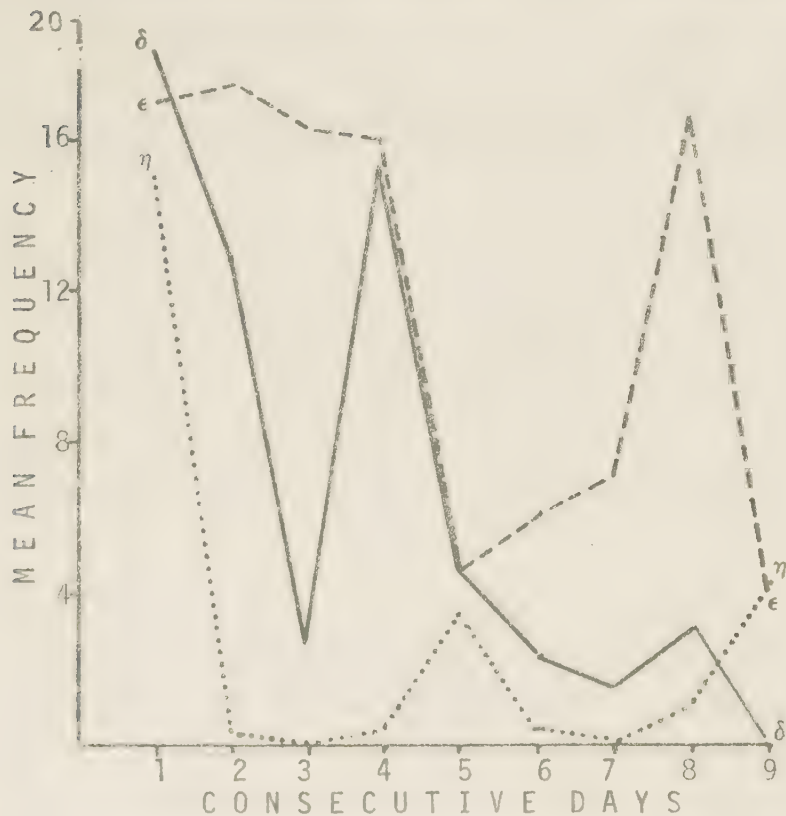


Fig. 2. Graphic representation of the distribution of responses over days (means) within Case I (males).

Regarding acts produced the interaction is graphically represented in Fig. 1 (females) and Fig. 2 (males). It is revealed that the females manifested a sharp rise in responsiveness during the sixth day. This phenomenon reflects the beginning of a reproductive phase. Further consulting Fig. 2 it is evident that this rise in female responsiveness coincided with a certain lowering in frequency pertaining to the males which remained until the eighth day when male ϵ^x begins to manifest an increase in responsiveness.

The notes made during the observations reveal that during the eighth and ninth day two attempts were made to establish territory and to spawn by female β and male ϵ and by female α and male η respectively. The latter pair never succeeded in establishing any territory. The crowded situation maintained in the aquarium probably prevented the establishment of two territories and in fact prevented any successful egg protection.

Table 3. Comparison between sex on the response distribution over days.

	Total	Acts produced	Acts received
Case I (N=9).			
females/males	r -.40	r -.69	r .22
females/day order	r_s .60	r_s .80	r_s .15
males/day order	r_s -.67	r_s -.73	r_s -.53

Case IIa (N=9).			
females/males	r .65	r .73	r -.07
females/day order	r_s .63	r_s .80	r_s .05
males/day order	r_s .87	r_s .43	r_s .81

Case IIb (N=5).			
females/males	r .55	r .28	r .59
females/day order	r_s .90	r_s .70	r_s .97
males/day order	r_s .90	r_s .70	r_s .80

^x The Greek letters refer to individuals not to positions in a ranking order.

Obviously these circumstances affected responsiveness differently with regard to the two sexes since males presented a negative relation to day order (Table 3) and a positive trend could be found with the females. This difference is most pronounced when considering the category of acts produced. Thus Fig. 3 reveals a shift in responsiveness between males and females on the sixth day (consider also Table 3 - acts produced).

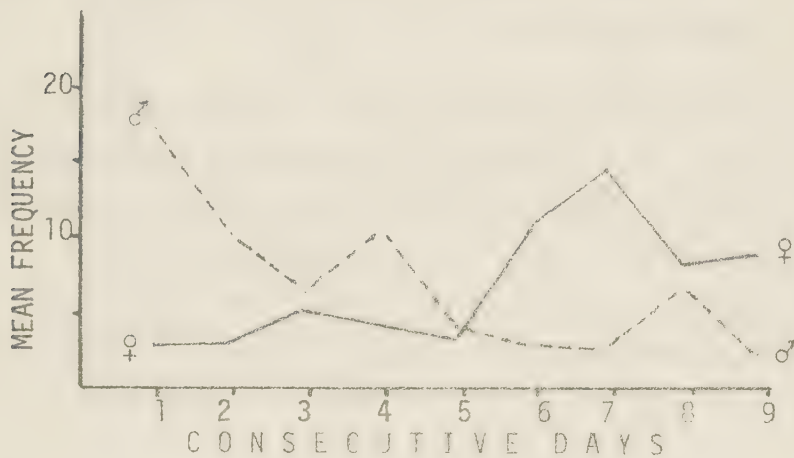


Fig. 3. Graphic representation of the response distribution over days by males and females within Case I (acts produced).

Fig. 4 reveals further that the interaction between days and individuals is influenced by a divergent development in responsiveness over days when high- vs. low-frequency individuals (individuals dichotomized along the median) are concerned. Again the trend is most conspicuous with the category of acts produced.

Although this is a minor source of variation (Table 4) it is interesting to note that in Fig. 4 these differences are small during the first, fourth and fifth days. Differences during the first days might be attributed to testing and establishment of power relations, whereas differences during the last days could reflect the earlier mentioned increase in activation.

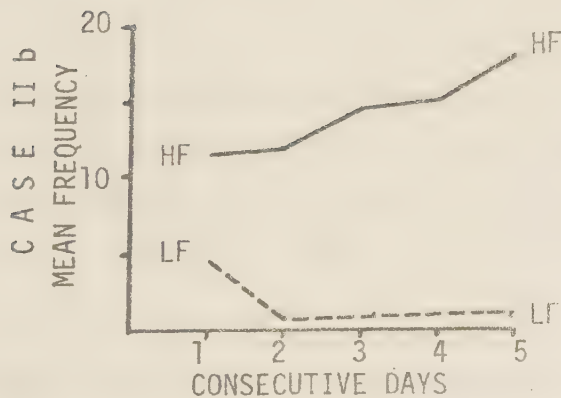
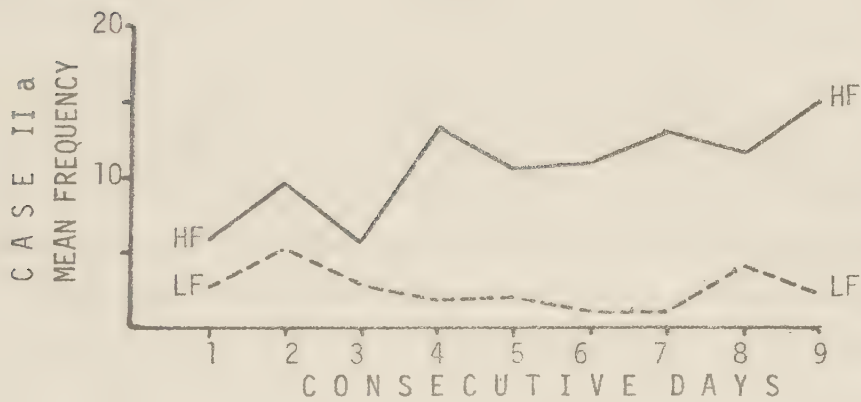
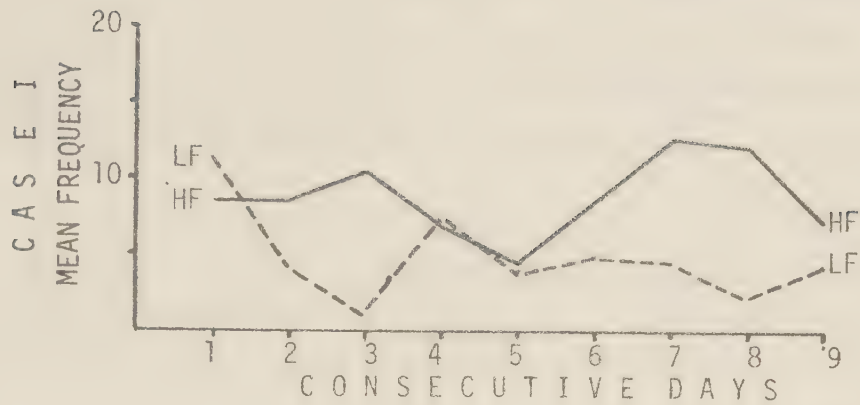


Fig. 4. Graphic representation of the response distribution over days by high vs. low frequency individuals within Case I, IIa and IIb (acts produced).

Table 4. Comparison between high- and low frequency fish (considered as sub-groups) on the response distribution over days.

	Total	Acts produced	Acts received
Case I			
High responsive/ low responsive (HR/LR)	r .20	r- .24	r .22
HR/day order	r _s .17	r _s .23	r _s .15
LR/day order	r _s -.23	r _s -.33	r _s -.53

Case IIa			
HR/LR	r- .39	r- .29	r .13
HR/day order	r _s .61	r _s .77	r _s .93
LR/day order	r _s .33	r _s -.35	r _s .13

Case IIb			
HR/LR	r -.05	r -.16	r -.21
HR/day order	r _s 1.00	r _s 1.00	r _s .70
LR/day order	r _s -.30	r _s .00	r _s -.20

Days × Individuals - Case IIa: In considering Case IIa (the established group) the interaction between days and individuals (Table 1) as with Case I is most pronounced within the category of acts produced ($p < .01$). The differences between categories are however not powerful enough to manifest any three-factor interaction (Days × Individuals × Categories).

Table 3 reveals that there is a positive relation between sexes over days and that both sexes manifest positive correlations with day order. Since the increase in frequencies over days is small, the latter trend seems, however, to be of less descriptive value.

Further a positive relation was obtained between sexes when acts produced were considered separately (Table 3), but this was not found with acts received. Within the category of acts produced a positive relation was also found between

females and day order and between males and day-order within the category of acts received. In both cases however, the increase in frequencies over days was not large enough to permit any definite conclusions to be drawn.

Thus in contrast to the findings from Case I it could be concluded that either a motivational timing between sexes (considered as sub-groups) has occurred, or the structural properties of the total group have been so far established that a rise in activation within one sub-group does not affect frequency-distribution over days in a manner equal to that of Case I.

The interaction between days and individuals is influenced by variation attributable of differences in responsiveness over days by high- vs. low-frequency individuals (Table 4) (Fig. 4 - acts produced). High frequency individuals manifest a positive relation with day-order while no relation with day-order is evident in the case of low frequency individuals. The trend is manifest in both categories although in the case of acts received the increase in frequencies is small over days.

Thus those fish classified ad hoc as high frequency individuals differed from those classified as low frequency individuals by an increase in responsiveness over days. This rise could be caused by hormonal fluctuations which either were not active in the low frequency group or the manifestations of which were depressed.

Finally an exception from the general low frequency trend was manifested by one of the female subjects (D) who showed a marked cyclic distribution of acts produced over days (Fig. 5) This phenomenon will be commented on later.

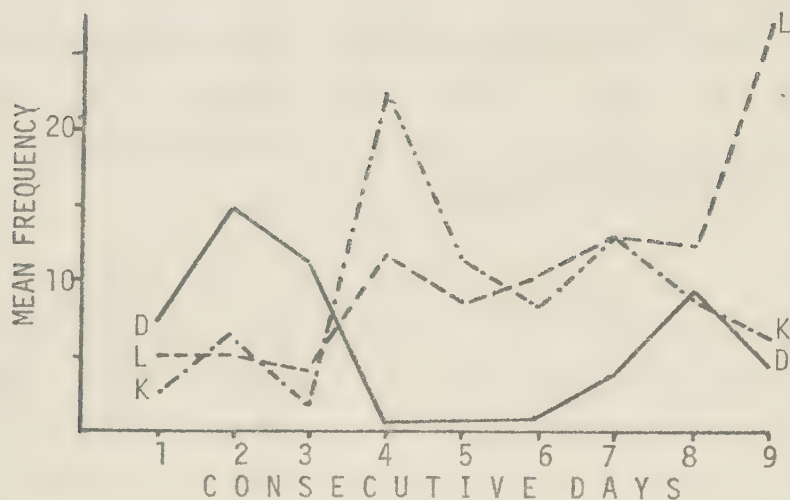


Fig. 5. Graphic representation of the response distribution over days by the females D, K and L within Case IIa (acts produced).

Days $\times$ Individuals - Case IIb: Considering the replica it was found that the interaction in Table 1 was seen most clearly this time within the category of acts received. As in Case IIa however the difference between categories in this respect did not manifest any significant three-factor interaction.

No relations were found between sexes when behavioural acts were considered over days (Table 3), both sexes however manifested positive relations with day order. Considering categories separately this trend was also found in the case of acts received. Thus in this respect the results obtained with the replica are in accordance with those obtained with the original study (IIa) but contrast with those obtained with Case I (where negative trends were found).

As in Case IIa no relations were found between high- vs. low-frequency individuals (Table 4), but a positive correlation between high frequency individuals and day order did exist. This trend was also evident when the category of acts

produced was considered separately. Thus, as in the original study a rise in responsiveness over days was revealed which was attributable to the high-frequency group.

Cluster analysis (elementary linkage^x) (McQuitty, 1957) performed on matrices of coefficients of correlations (r) obtained by pairwise comparisons between days over individual frequencies of behavioural acts, yielded further information in three instances:

(1) An analysis performed on the total frequencies (acts produced and received) in Case I revealed two clusters, namely: day 1,2,4 vs. 6,7 and 9 (min. similarity: $r=.71$). This confirms the earlier findings that in Case I day 6 appears to have been a turning point.

(2) An analysis performed on acts produced in Case IIa revealed two clusters, namely: day 1-3 vs. 4-9 (min. similarity: $r=.74$). This shift may be caused by an increase in activation by females K and L, or a decrease in activation by female D (Fig. 5).

(3) An analysis performed on acts received in Case IIb revealed that day 1 was unrelated to the rest of the days (min. similarity $r=.74$). The main reason for this phenomenon seems to be the low frequencies of male A during the first day (Fig. 6). This otherwise high frequency male apparently kept away from prolonged interaction during the first day.

Comparison between days over individual frequencies (Table 5) further yields a measure of the stability of response distribution. Thus Table 5 shows a comparatively low degree of consistency with Case I, while the reverse holds for Case IIa and IIb.

^x Among the various kinds of cluster analyses now available the elementary analysis was chosen because of its simplicity and stability (Anderberg, 1973).

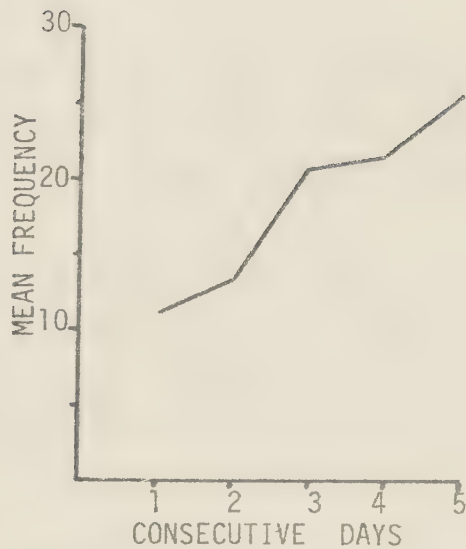


Fig. 6. Graphic representation of the response distribution over days by male A with Case IIb (total: acts produced + received).

Table 5. Mean correlations between all days over individual frequencies of responses (means obtained via Fisher z_r).

	Total	Acts produc.	Acts received
Case I (N= 6).	.17	.16	.49
Case IIa (N=11).	.60	.57	.60
Case IIb (N=11).	.68	.84	.58

Table 6. Mean correlations between adjacent days over individual frequencies of responses (means obtained via Fisher z_r).

	Total	Acts produc.	Acts received
Case I (N= 6).	.51	.52	.49
Case IIa (N=11).	.69	.77	.64
Case IIb (N=11).	.79	.87	.61

Comparisons between adjacent days over individual frequencies of responses (Table 6) yield information about sudden changes in response distributions. In this respect as well the degree of consistency was low in Case I but high in Case IIa and IIb.

It seems clear that in spite of individual differences and differences between sub-groups there was an over-all high degree of stability with regard to the relative response distribution within what has been called the established group (Case IIa and IIb). In this respect it contrasts with the establishing group (Case I). The result is also in accordance with the reasoning that hormonal fluctuations do not seem to affect response distribution as much in Case IIa and IIb as in Case I.

These differences may have been a product of differences in total life area (although this has been checked as far as possible within the limits of available resources). It may be a product of individual characteristics, but it may also be a product of more or less firm group structure.

(2) Qualitative analysis.

The qualitative analysis concerns the direction of interaction (choices). It must be remembered that data was obtained only from Case IIa and IIb (the established group).

In considering high- and low frequency individuals as sub-groups no differences were found with regard to preferred interaction in terms of first choices (most frequent choice). On the contrary in both Case IIa and IIb a trend towards making first choices against high frequency fish was evident. Thus the total number of acts produced or received could not be considered as a discriminating predictor of choice preference.

It is thus evident that although high and low frequency individuals (as sub-groups considered) manifest different trends in responsiveness over days (as was found in the quantitative analy-

sis), the low frequency group do not produce and receive these acts primarily within their own sub-group.

In comparison sex seems to be a far more potent predictor. Thus both in Case IIa and IIb a tendency for the most preferred fish to be of the same sex was found (Case IIa: $P_{\text{total}} = .01$ /Fisher/; Case IIb: $P_{\text{total}} = .06$). In Case IIa this tendency is most marked when considering acts produced where $P_{\text{acts produced}} = .01$ ($P_{\text{acts received}} = .06$) and in Case IIb the trend was found to be equally evident in both categories ($p < .05$). Considering acts produced the trend remained even for the secondary choices (Case IIa: $P_{\text{acts produced}} = .01$; Case IIb: $P_{\text{acts produced}} = .05$).

It must be remembered that in the quantitative analysis it was found that the development of responsiveness over days in these cases not differ between sexes. Thus it seems clear that, although the number of behavioural acts produced and received over days differs with regard to overall level of frequency, the direction of behavioural acts differs with respect to sex.

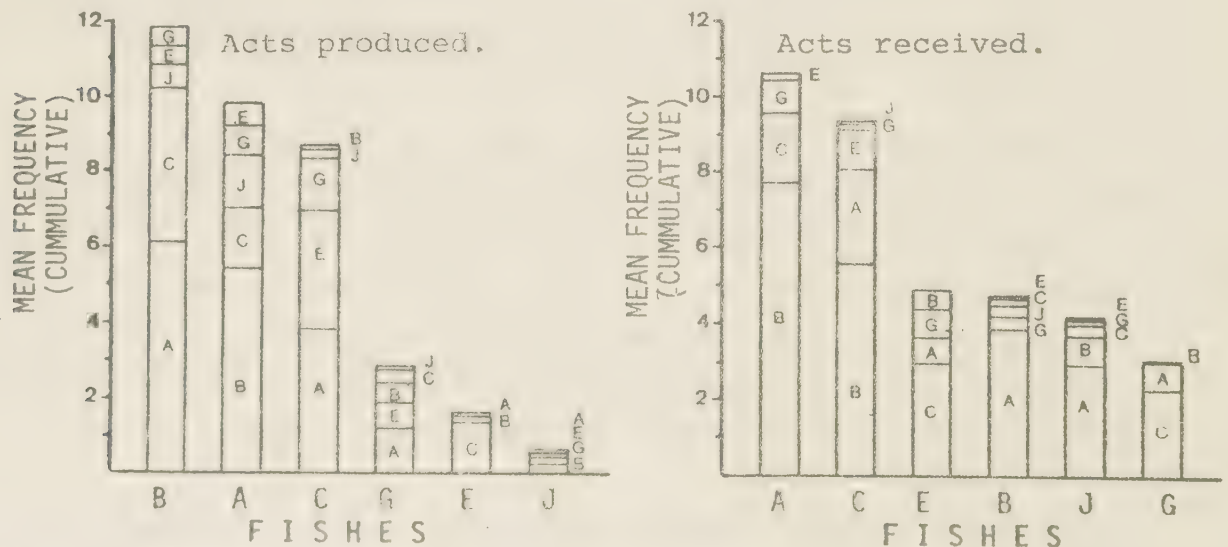


Fig. 7. Direction and magnitude of interaction between fish within Case IIa (males).

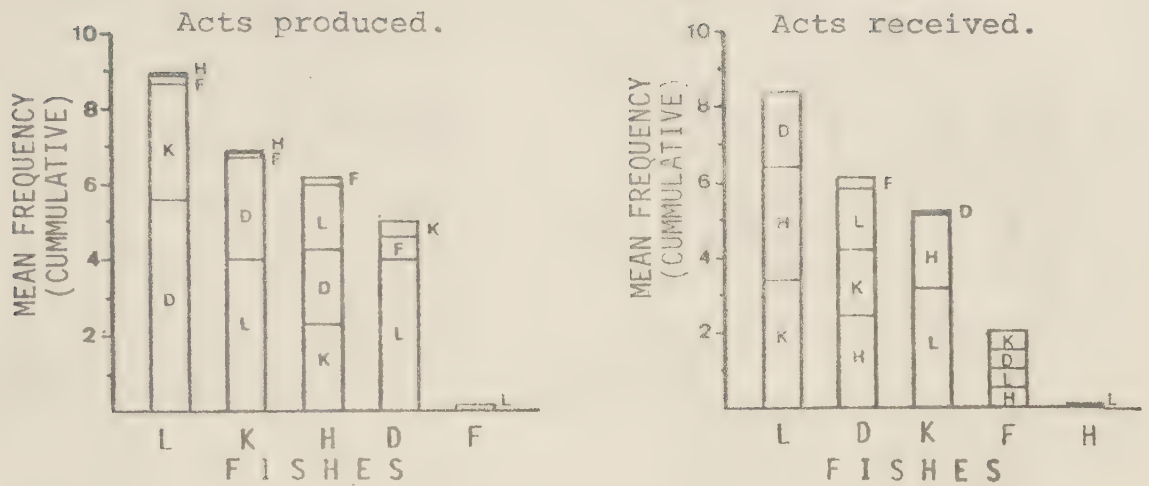


Fig. 7. Direction and magnitude of interaction between fish within Case IIa (females).

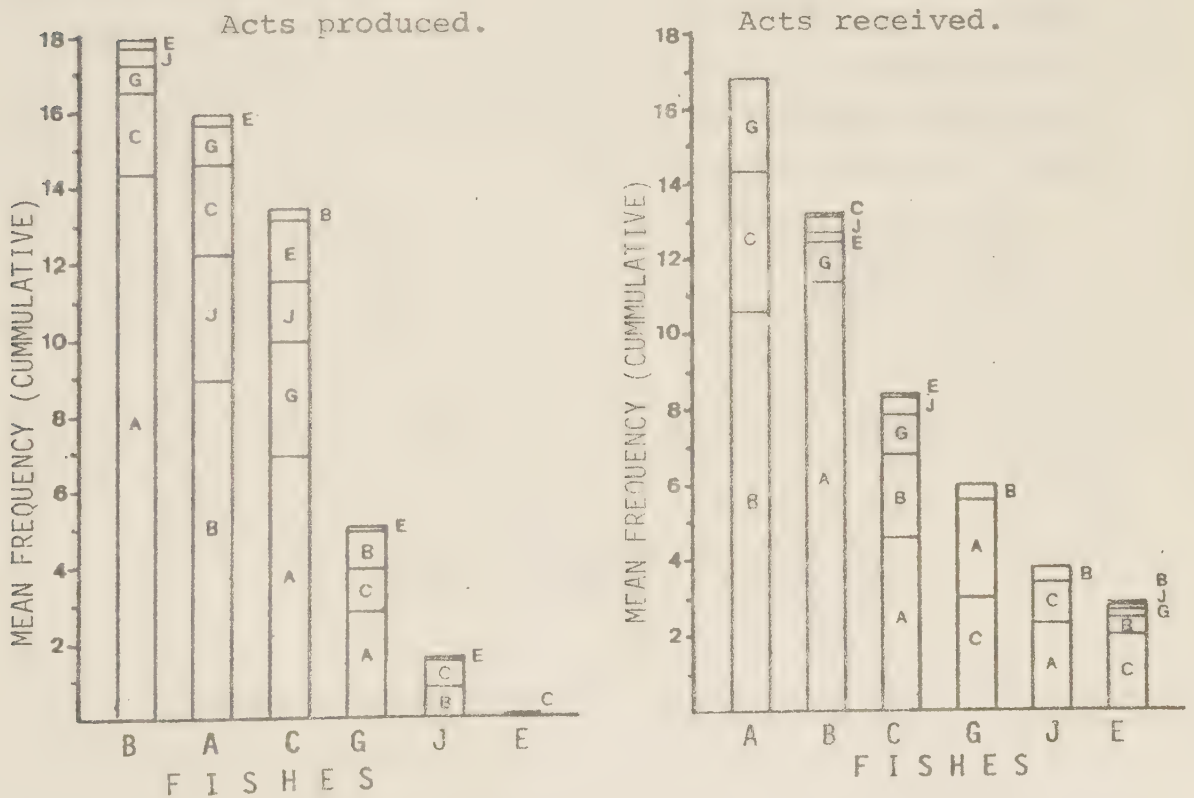


Fig. 8. Direction and magnitude of interaction between fish within Case IIb (males).

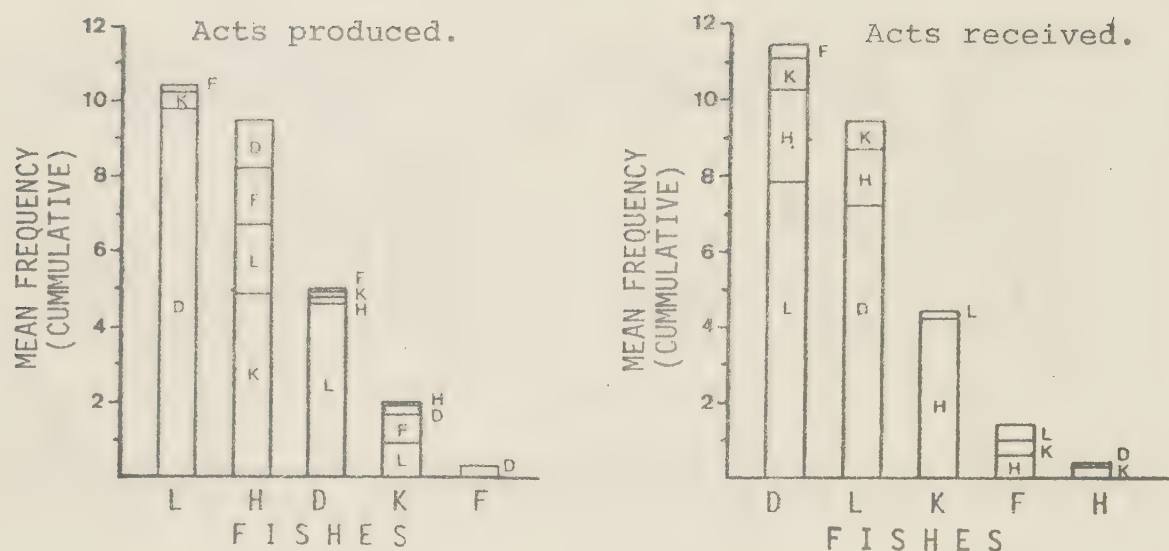


Fig. 8. Direction and magnitude of interaction between fish within Case IIb (females).

Within each sex, differences were found with regard to the extent that certain individuals interacted with each other. From Fig. 7 and 8 the system of interaction was deduced for the males in Case IIa and IIb and the females respectively. The analysis was made with regard to first choices (Fig. 9 and 10).

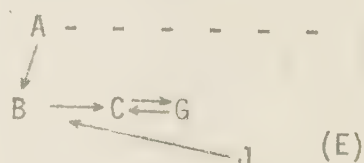
CASE IIa (males)

Acts produced.



CASE IIb (males)

Acts produced.



The dotted line indicates an overall tendency to choose A as major target.

Acts received.



Acts received.

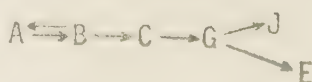


Fig. 9. Graphic representation of the system of interaction between males within Case IIa and IIb.

CASE IIa (females)

Acts produced.

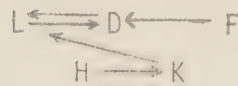


Acts received



CASE IIb (females)

Acts produced.



Acts received



Fig. 10. Graphic representation of the system of interaction between females within Case IIa and IIb.

Considering the males they system of interaction could be ascribed the attributes of a hierarchy in its semantic meaning (Dawkins, 1976) although not a linear hierarchy. Regarding the females the interaction tended to concentrate around a nucleus of interaction between D, K and L.

Notes obtained during the observations reveal that in the aquarium each male except J occupied a standing place which it retained throughout Case IIa and IIb. Regarding fish A this standing place could without doubt be considered as a territory covering approximately 1/3 of the total area. For the rest of the males no territories could be identified and no territorial defence against any other fish than A was noted.

A situation which occurred frequently in the aquarium was an attack from A on B, and a joint counterattack on A released by B and followed up by C and often also by G. This situation is graphically represented in Fig. 11.

The resolution of these attacks was often that A turned back to the inner part of its territory while fish B turned around to produce charges against fish C. This sequence was sometimes followed by an attack from C on G, which in rare cases could be followed by an attack on E by G. These sequences are represented in Fig. 12.

Female H presented an interesting case. This was the smallest fish in the sample, but as can be seen in Figs. 7 and 8 it produced a large portion of the total behavioural acts, while it received proportionally much less. Female H was the only fish tolerated by A in its territory, where H functioned as kind of a gate-keeper against the circulating fish (J and F) as well as against the females D, K and L. Occasionally it followed A in attacks on the other males (not joint attacks), occasionally H attacked the females D, L and K by herself outside the territory. No sign of mating between A and H was ever recorded.

It has been argued that it may be dangerous to lump together frequencies of responses and to interpret the totals in terms of effectiveness on some general social parameter (in the case of dominance see Brown, 1975). It has also been shown in an earlier article in this series that interactive relationships complicate the interpretation of the totals (Hansson, 1978). The above analysis was therefore completed with an analysis of response profiles, that is, pairwise comparisons between fish on acts produced or received over the rest of the sample (mutual interactions between the two fish compared were not considered). It should then be possible to pool fish together in terms of similarity of response-profiles and to compare the result with the above analysis.

When recording both acts produced and received within each period of observation there will however, be two interaction matrices, one for acts produced and one for acts received. If these matrices are organized so as to be read along the rows the columns will yield information about the opposite category independent of the information obtained within the matrix of that category (Fig. 13).

		Receiving fishes		
Producing fishes		A	B	C
	A		5	6
	B	7		8
	C	9	10	
	D	11	12	13

Fig. 13. Example of an interaction matrix on acts produced. If read along the rows this matrix yields information of acts produced against individuals listed on top of the matrix and by those listed along the ordinate of the matrix. If read along the columns the matrix yields information on acts received by those listed on top of the matrix. This measure should be independent from those measures on acts received recorded within the focal sessions and revealed within the matrix of acts received.

Thus for each fish two measures on each category were obtained, one obtained from the actual sessions of observations when the particular fish was focal and the other derived from the entire period and deduced from the records of the opposite category. In comparison this latter measure could then be considered as associated with the reliability of the observations. In the following discussion we should distinguish between original measures and the latter measures (secondary measures).

Significant relations between response profiles of the individuals from Case IIa and IIb were expressed as means between correlations on original and secondary measures (separately obtained) in Table 7.

Table 7. Correlations between response profiles of individual fish (mutual interaction between fish not included). Recorded coefficients represent means from correlations between original and correlations between secondary measures (see text) (means obtained via Fisher z_r). N: 9. Underlined coefficients indicate $p < .05$.

Subject	AB	AC	AG	AH	BC	BG	BH	BJ	CG	CH	DF	DJ	DK	DL	EF	EG	FL	HK	HL	JK	KL
Sex	♂♂	♂♂	♂♂	♂♀	♂♂	♂♂	♂♀	♂♂	♂♂	♂♀	♀♀	♀♂	♀♀	♀♀	♂♀	♂♂	♀♀	♀♀	♀♀	♂♀	♀♀
Acts produced																					
Case IIa	.70	-.23	.34	-.36	.50	.66	-.44	-.16	.85	-.42	.84	.71	.92	.29	-.08	-.15	.89	.91	.83	.74	.94
Case IIb	.72	-.19	.72	-.17	.83	.93	-.37	-.20	.75	-.49	-.07	.28	.19	.27	.08	-.07	.82	.34	.19	.20	-.13
Acts received																					
Case IIa	-.01	.95	.36	.90	.85	.32	.98	.84	.37	.84	.47	.04	.81	.95	.26	.91	.59	.33	-.28	.54	.35
Case IIb	.12	.88	.41	.27	.96	.42	.84	.58	.87	.55	-.09	-.04	.04	.80	.72	.90	-.36	.73	.23	.38	.08

The correspondence between Case IIa and IIb should be considered as high. The most notable exceptions are found with pairs D/F, D/K, H/K, H/L and K/L. Although the special role played by fish H in the group should be considered, a tentative conclusion may be that the response profiles of the females show less stability over time than the profiles of the males.

In some instances an association is found between the response profiles of males and females, namely with A/H, B/H, C/H, D/J, E/F and J/K. The correlations between males and the female H are all to be found when considering the acts received; the special role played by H will explain these associations. Regarding E, J and F, these are all low responding individuals (Figs 7 and 8) (J when regarding acts produced), in these instances the correlations might be of less descriptive value.

The pattern of correlations revealed confirms in general the crude graphic interpretation of first choices discussed earlier (Figs 7 and 8; Figs 9 and 10). For example, pair A/B correlates as regards acts produced (both produce against C and G) but not as regards acts received (A primarily receives from C and J while B does not). In the same manner A/C correlate regarding acts received but not regarding acts produced (both receive from B, but A produces against B while C does so against E and G), etc.

Further the correlation matrices underlying Table 7 were treated by means of cluster analysis (elementary linkage, min. similarity: $r=.67$).

The resulting cluster analyses are presented in Figs 14 and 15. Notice that these figures include analyses obtained from correlations between original measures, secondary mea-

asures and finally means between the former correlations (r_{original} and $r_{\text{secondary}}$). Although there are some differences between the analyses based on original vs. secondary measures, the changes are small and do not disturb the general trends.

	Original measures	Secondary measures	Means (r_{original} and $r_{\text{secondary}}$)
Total (acts produced + received)	A=B—J E—G=C D=K H=L—F	A=B—G E=C K=D—L H	A=B—G—C J E H—K=D—L—F

Acts produced.	C=G A=B (E=J) D=F H—K=L	C=G A=B H D—K=L—F J(♂)	C=G A=B (♂) J—K=L—F D H

Acts received.	C=A—H(♀)—B—J E=G L=D—K	B=H(♀)—J C=A E=G L=D—K	H=B—J A=C E=G L=D—K

Fig. 14. Results of cluster analysis on similarity between individual response profiles of fish within Case IIa. Dotted lines indicate high correlations excluded by the analysis (see text for explanation).

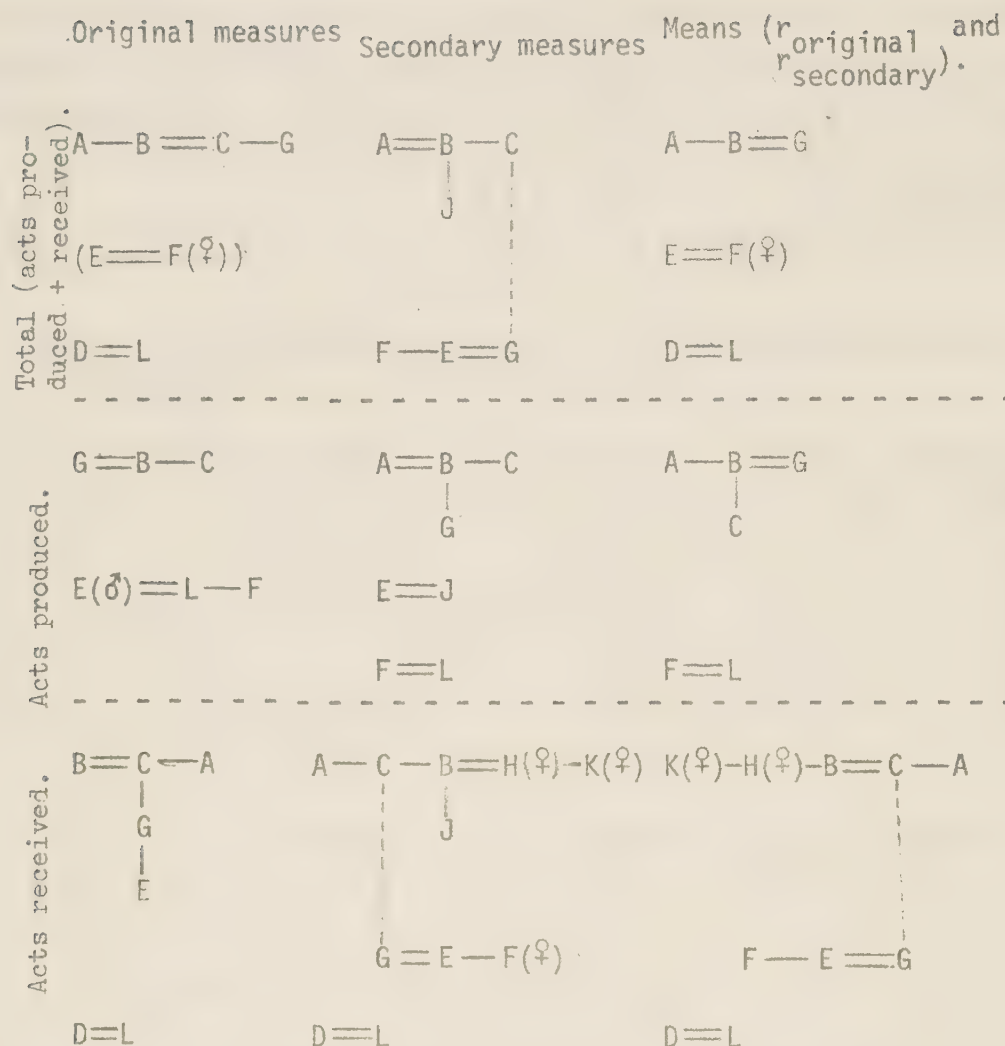


Fig. 15. Results of cluster analysis on similarity between individual response profiles of fish within Case IIb. Dotted lines indicate high correlations excluded by the analysis (see text for explanation).

It must also be remembered that the kind of cluster analysis which is applied here yields a certain bias when used on these matrices. The matrices embrace highly separated parts which are associated within themselves by strong positive coefficients. The elementary linkage analysis will then result in loss of some strong associations within parts of the matrix thereby yielding in some cases a false impression

of short chains (in some cases interconnections between what otherwise appears to be mutual pairs has been indicated in the figures). This phenomenon should be noted since the opposite condition (long chains) occurs more commonly.

As with the discussion in relation to Table 7 the following discussion is based on the cluster analyses representing means. The following conclusions may be drawn:

(1) The main basis for clustering is according to sex. This general rule is most clearly seen with the totals. The trend is however, also evident when considering separately acts produced and received.

(2) Minor trends were found showing that fish cluster according to similarities in response frequency (cf. Figs. 7 and 8) (cf. the quantitative analysis). Thus, considering acts received the low frequency fish E, F and G tend to associate. Considering the totals and acts produced A and B tend to associate (high frequency fish) as do C and G (to a lesser degree high frequency fish). The trend to associate according to similarities in response frequency is, however, not completely clear, since there are low frequency fish which associate with high frequency fish (e.g. J and F). This may partly depend on the interactive relationship between acts produced and received as described earlier (Hansson, 1978) but also on the special situation in this aquarium (cf. fish H).

(3) There is an over-all high correspondence between Case IIa and IIb.

(4) The cluster analysis yields a picture similar to that obtained from direct scanning of the interaction between fish as graphically represented in Figs 9 and 10. Thus, an analysis

based on comparisons between response profiles and an analysis of direct interaction yield in this case similar results

Any suggestion of group structure must embrace the implicit assumption of stability over time not only as regards the relative distribution of responses (which has been commented on in connection with the quantitative analysis) but also with regard to direction of responses. Therefore comparisons were made for each individual between each day on relative interaction with other fish.

Table 8. Individual consistency on direction of interaction over days (totals: acts produced + received). N:10. Underlined coefficients indicate $p < .05$.

Subject	A	B	C	D	E	F	G	H	J	K	L
Case IIa											
$\bar{r}_X$	<u>.90</u>	<u>.80</u>	<u>.73</u>	<u>.76</u>	<u>.70</u>	<u>.08</u>	<u>.77</u>	<u>.32</u>	<u>.52</u>	<u>.44</u>	<u>.64</u>
total rank	<u>1</u>	<u>5</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>11</u>	<u>10</u>	<u>7</u>	<u>9</u>	<u>6</u>	<u>3</u>
sex	♂	♂	♂	♀	♂	♀	♂	♀	♂	♀	♀

Case IIb											
$\bar{r}_X$	<u>.89</u>	<u>.99</u>	<u>.75</u>	<u>.82</u>	<u>.66</u>	<u>.09</u>	<u>.65</u>	<u>.50</u>	<u>.55</u>	<u>.58</u>	<u>.96</u>
total rank	<u>1</u>	<u>2</u>	<u>3</u>	<u>5</u>	<u>11</u>	<u>10</u>	<u>7</u>	<u>6</u>	<u>9</u>	<u>8</u>	<u>4</u>
sex	♂	♂	♂	♀	♂	♀	♂	♀	♂	♀	♀

The correlations expressed in Table 8 represent means of correlations between all days. It can be seen that all correlations are positive and with one exception fairly strong. Consequently it could be concluded that there is some consistency in the direction of interaction over days.

Certain correlations in Table 8 do not reach the limit of significance, namely those pertaining to fish F, H, J and K. Considering the ranking numbers (obtained from total

frequencies) revealed in Table 8 it should be evident that none of these fish represent high frequency individuals. It is further evident that J is the only male which shows less stability over days. In terms of totals this is also a low frequency fish (the total is composed of low frequency status on behalf of the acts produced and medium status regarding acts received). A reconsideration of Figs 14 and 15 further reveals that J is less linked to the male group than the rest of the males. Notes made during the observations also reveal, as was earlier mentioned, that J spent much of its time circling around in the aquarium. In principle this reasoning also holds for F.

With exception of these fish it might still be suggested that the behaviour of the males is more stable over days than that of the females. This confirms the earlier findings (cf. p. 28). Reconsidering Figs. 14 and 15 the females seem to constitute a fairly closed group, but from Table 8 it seems as though the focus of the group changes over days (and from Case IIa to Case IIb especially taking into consideration the rankings of the female K. Consider also Fig. 5 in connection with the quantitative analysis of Case IIa and in this figure female D). It has previously been suggested that the social relations of the females could be more influenced by motivational fluctuations than those of the males and thus result in a larger amount of pairwise interaction (cf. p. 24). Thus far the figures on Table 8 seems to confirm this suggestion.

Summary of results - the quantitative analysis.

(1) Regarding the distribution of totals, differences were observed between fish and between days, but not between the categories acts produced vs. acts received.

(2) Interactions between days and individuals were further revealed. Regarding Case I (the group under establishment) interactions also appeared between days, individuals and categories.

(3) It was also found that individual trends over days reflecting fluctuations in motivational states affected the total social structure of Case I more powerfully than those of Case IIa and IIb (the established group).

(4) Fluctuations in motivation were also reflected by different trends over days between males and females in Case I but not in Case IIa and IIb.

(5) Within the established group on the other hand different trends were found over days in respect to high- vs. low frequency fish.

(6) The stability of the response distribution over days was found to be high for individual fish within the established group (Case IIa and IIb) but was comparatively lower within the group under establishment (Case I). The same trend was evident when comparing adjacent days.

(7) Individual levels of frequency found in Cases IIa and IIb were shown to correspond fairly well.

Summary of results - the qualitative analysis.

(1) A general preference for making most frequent choices of individuals belonging to the same sex, rather than according to a dichotomization between high vs. low frequency individuals was revealed.

(2) In both Case IIa and IIb what semantically could be called a branching hierarchy among males was observed. On the other hand the female interaction was found to be mainly pairwise.

(3) Similarities between responses profiles were considered. In this respect the results obtained earlier by an inspection of the totals were generally confirmed.

(4) In the case of response profiles comparatively good agreement was found between Case IIa and IIb, although it was not an exact correspondence. In general agreement between Case IIa and IIb was lower in the case of females than males.

(5) Matrices of correlations obtained from comparisons between response profiles were treated by means of cluster analysis. Clusters were found to be separated mainly according to sex. Further tendencies to cluster according to similarities in frequency of responses were observed.

(6) Consistency of choices over days was generally considered to be high, although comparatively lower with respect to the females than the males. We concluded that this female trend might depend on preference for females to interact pairwise reflecting a weaker group structure.

C o n c l u s i o n s

External validity.

When considering social relations between fish in an aquarium the question of validity is crucial. Although the aquarium may represent a more or less genuine miniature replica of nature it still constitutes an enclosed area. Special delimited niches exist in nature, but these are part of the ecology to which fish are adapted and not artificial demarcations imposed upon fish by an experimenter. Dominance as a natural phenomenon should best be studied in nature.

Several explanations of the function of social dominance have been suggested since the pioneering studies were made by Schjeldrup-Ebbe in the 1920s. Regarding the evolution of dominance hierarchies it could on the other hand with some generality be asserted that they appear because less successful animals learn not to contest access to resources when they are unlikely to win thus saving time and energy (Clutton-Brock and Harvey, 1976). In this way the problem of dominance may be analogous to that of territory (Wilson, 1971). Further a switch has been noticed from territoriality at low population density to dominance behaviour at high density in many species (e.g. Archer, 1970; see also Wilson, 1975 for review).

Although a transition from territoriality to dominance with increased population density could imply the appearance of an unnatural behaviour (as argued by Gartlan, 1968) dominance in such cases still constitutes a latent behaviour of the species.

The fish used in the studies reported here, form pairs and establish territory under natural conditions (Bergmann, 1971). The natural behaviour is broken down by the high density which was prevalent in the aquaria and replaced by another behaviour, which is less accessible, but still a part of the behavioural repertoire.

Thus studies of dominance in aquaria still have a heuristic value, and the relevant question when discussing external validity should be, whether a capacity to form dominance relations could be taken for granted and if so, what bearing this may have on the evolutionary history of that particular species.

Internal validity.

It might be argued that dominance in an aquarium as reported in these studies, does not even reflect a latent behaviour but constitutes an artefact (statistical or in some way an experimental artefact). This argument could be interpreted in at least three ways:

- (1) The differences in frequency of behavioural acts produced and received by individual fish reflect individual variation unrelated to a concept of group structure.
- (2) The differences observed stem from temporary motivational fluctuations and reflect only temporary formations which could not be described as dominance structures.
- (3) The differences observed reflect pairwise interaction at different levels of frequency, where the differences between pairs might be large.

Although these arguments certainly are interconnected, and not clearly separated from the question of reliability it is convenient to discuss them separately since their content is slightly different, and in connection with validity since they all concern the applicability of the dominance concept.

The first argument is weak since it should be clear to anyone that the variation reported in these studies is systematic.

Before discussing the second and third arguments however it should be considered that the data do not support any idea of an over-all hierarchy of dominance. It is evident that interaction is sex-bound; consequently each sex should be considered separately with regard to dominance.

In considering the second argument it was found that the stability of individual frequencies over days was low in the group under establishment (Case I), but high in the established group. Further individual choices within the established group remained fairly stable when considering the male sub-group both over days within Case IIa and IIb (the female group, however, manifested somewhat lower stability in this respect). In answering the second argument it should however be clear that on the whole sufficient consistency of data has been demonstrated.

As for the third argument, the relation between the males B, C, G, E, J could hardly be described as pairwise interaction, although the data do not altogether disprove a suggestion of basic nuclei of pairwise interaction. On the other hand, it has already been noted that the relations among the females may be described as pairwise although even in this case no clear cut pairwise interaction has been demonstrated (cf. the results obtained by Weeber and Weeber, 1975 on Convict cichlids).

It might be suggested that male A in Case IIa and IIb plays the classical role of a despot (Baerends, et al., 1950). It could even be argued that there was one male and one female despot (A and H) in the sample. This reasoning is however not entirely in accordance with the data. In the first place A could not be considered an overall despot since its interaction with the females (including female H) was low. Secondly

fish A and H dominated a territory but were not in absolute dominance outside the territory.

Thus the third argument seems to be only partly true, and we are left to agree with the recurrent opinion of the complexity of the concept of dominance (e.g. Clutton-Brock and Harvey, 1976). For one thing the social system of the males tends to support the idea of social dominance. On the other hand it might be suspected that the female interaction is based on pairwise interaction. Finally including the behaviour of male A, we have in the end obtained the simultaneous appearance of a territory, a dominance-order and pairwise interaction.

Reliability.

The classical way to approach observer reliability is via the construction of an agreement index between two or more observers. For practical reasons this could not be done. Some months after these observations had been completed however a follow-up study was made which centered around the problem of the impact of relative degrees of crowding on the group behaviour of this fish (Johansson, 1975). The general findings were in accordance with those found in the earlier study.

The stability of behaviour manifested over days which was discussed in connection with internal validity, could further be considered not only as a measure of individual consistency but also as a measure of observer reliability. In this way, since the behaviour manifested within Case IIa and IIb was associated with high stability a corresponding high reliability of measures could be concluded. In this respect the high correspondence of behaviour manifested on adjacent days is especially informative. This is further confirmed by the consistency manifested in connection with di-

rection of choices. In Case I the measures of consistency of behaviour did not, on the other hand, reach the limit of significance. Therefore in this respect nothing could be said about the reliability of that study.

Further, in considering Case IIa and IIb a high degree of correspondence was found between these studies.

It should also be remembered that in the discussion on the direction of choices within Case IIa and IIb we obtained two measures of acts produced and received respectively- one pertaining to observations made within the focal periods on one or the other category (original measures) and one measure pertaining to observations on the opposite category deduced from the total observations on the first category (secondary measures). As is revealed in Table 9 the correspondence between the frequency of responses to and from preferred individuals is high in both Case IIa and IIb.

Table 9. Correlations between original and secondary measures on each day over individual choices. N 11. Underlined coefficients indicate $p < .05$.

Case IIa

Day	1	2	3	4	5	6	7	8	9	$\bar{X}$
$r_{\text{produc.}}$	.61	<u>.89</u>	.46	<u>.89</u>	<u>.89</u>	<u>.88</u>	<u>.93</u>	<u>.80</u>	<u>.90</u>	<u>.84</u>
$r_{\text{receiv.}}$	<u>.71</u>	<u>.86</u>	.11	<u>.92</u>	<u>.77</u>	<u>.93</u>	<u>.94</u>	<u>.83</u>	<u>.78</u>	<u>.82</u>

Case IIb

Day	1	2	3	4	5	$\bar{X}$
$r_{\text{produc.}}$	<u>.84</u>	<u>.82</u>	<u>.85</u>	<u>.90</u>	<u>.86</u>	<u>.86</u>
$r_{\text{receiv.}}$	.47	<u>.73</u>	<u>.82</u>	<u>.83</u>	<u>.89</u>	<u>.78</u>

It should be clear that the data in Table 9 should also be considered to reflect the effectiveness of the focal sampling. The trends found within the focal sessions are supported by those found in the entire material.

In summary, the data indicate a state of high reliability within and between Case IIa and Case IIb, while no direct measures of reliability of Case I could be deduced. A suggestion of systematic error on the part of the observer is refuted by the findings of Johansson, 1975.

G e n e r a l c o n c l u s i o n s

The advantage of the focal method have been discussed. It was found that it may constitute a useful tool for systematic observations within the field of social ethology. It was found that in situations such as the one used in this study the method offers good opportunities to obtain large and differentiated information about ongoing social interaction and is associated with satisfying reliability of measurement.

References

- Abramovitch, R. (1976). The relation of attention and proximity to rank in preschool children. In M.R.A. Chance & R. R. Larsen (Eds, The social structure of attention.
- Altmann, J. (1974). Observational study of behaviour: sampling methods. Behaviour, 49, 227-267.
- Anderberg, M. (1973). Cluster analysis for application. London: Academic Press.
- Archer, J. (1970). Effects of population density on behaviour in rodents. In J.H. Crook (Ed.), Social behaviour in birds and mammals. London: Academic Press.
- Arrington, R.E. (1943). Time sampling in studies of social behaviours: a critical review of techniques and results with research suggestions. Psychol. Bull., 40, 81-124.
- Baerends, G.P. & Baerends-van Roon, J.M. (1950). An introduction to the study of the ethology of cichlid fishes. Behaviour, suppl., 1.
- Bergmann, H.H. von (1971). Untersuchungen zur verhaltensentwicklung beim Segelflosser (*Pterophyllum scalare* Cuv. & Val., Cichlidae). Zeitschr. Tierpsychol, 29, 343-388.
- Box, H.O. (1973). Organisation in animal communities. London: Butterworths.
- Brown, J.L. (1975). The evolution of behavior. New York:Northon & Co.
- Clutton-Brock, T.H. & Harvey, P.H. (1976). Evolutionary rules and primate societies. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge: Cambridge Univ. Press.
- Christiansen, J.T. (1975). Darwin, Lorenz, Reventlow et videnskabsteoretisk studium. In K.B. Madsen (Ed.), Psykologi og videnskabsteori. København: Munksgaard.
- Cooper, E.S., Costello, A.J., Douglas, J.W.B., Ingleby, J.D. & Turner, R.K. (1974). Direct observation? Bull. Br. psychol. Soc., 27, 3-7.

- Dawkins, R. (1976). Hierarchical organisation: a candidate principle for ethology. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge:Cambridge Univ. Press.
- Erickson, J.G. (1967). Social hierarchy, territoriality and stress reactions in sunfish. Physiol. Zoöl., 40, 40-48.
- Frey, D.F. & Miller, R.J. (1972). The establishment of dominance relationships in the blue gourami (*Trichogaster trichopterus*, Pallas). Behaviour, 42, 8-62.
- Gartlan, J.S. (1968). Structure and function in primate society. Folia Primatologica, 8, 89-120.
- Greenberg, B. (1947). Some relations between territory, social hierarchy and leadership in the sunfish (*Lepomis cyanellus*). Physiol. Zoöl., 20, 267-299.
- Hansson, S.B. (1978). Notes on the ethological method of observation. I. Selection of behavioural units. Mimeo. Lund University, Lund.
- Iersel van, J.J.A. (1953). An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour, suppl. 3.
- Jenkins, T.M. (1969). Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav., Monogr., 2, 57-123.
- Johansson, L.A.G. (1975). En studie över aggressivt beteende och hur det förändras vid kontakt med nya individer och vid ändrad miljö hos Pterophyllumscalare (Pisces: Cichlidae). Mimeo, Lund University, Lund.
- Lehrman, D.R. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. Quart. Rev. Biol., 28, 337-363.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vögels. J. Ornithol., 83, 137-213, 289-413.
- Lorenz, K. (1965). Evolution and modification of behavior. Chicago: Univ. Chicago Press.

- Masure, R.A. & Allee, W.C. (1934). The social order in flocks of common chicken and the pigeon. Auk., 51, 306-327.
- McGrew, W.C. (1972). An ethological study of children's behavior. New York: Academic Press.
- McQuitty, L.L. (1957). Elementary linkage analysis for isolating orthogonal and oblique types and typal relevancies. Educ. and Psychol. Measurement, 17, 207-229.
- Menzel, E.W. jr. (1969). Naturalistic and experimental approaches to primate behaviour. In E.P. Willems & H.L. Raush (Eds), Naturalistic viewpoints in behavioural research. London: Holt, Rinehart & Winston.
- Myrberg, A.A. jr. (1972). Social dominance and territoriality in the bicolor damselfish, *Eupomacentrus partitus*, Polay (Pisces, Pomacentridae). Behaviour, 41, 207-231.
- Newston, D. & Enquist, G. (1976). The perceptual organisation of ongoing behavior. J. exper. Psychol., (in press).
- Richards, S.M. (1974). The concept of dominance and methods of assessment. Anim. Behav., 22, 914-930.
- Simpson, M.J.A. & Simpson, A.E. (1977). One-zero and scan methods for sampling behaviour. Anim. Behav., 25, 726-731.
- Syme, P.E.K. (1974). Competitive orders as measures of social dominance. Anim. Behav., 22, 931-940.
- Weeber, P.G. & Weeber, S.P. (1975). The effect of female colour, size, dominance and early experience upon mate selection in male convict cichlids, *Cichlasoma nigrofasciatum*, Günther (Pisces, Cichlidae). Behaviour, 56, 116-135.
- Willems, E.P. (1969). Planning a rationale for naturalistic research. In E.P. Willems & H. Raush (Eds), Naturalistic viewpoints in psychological research. New York: Holt, Rinehart & Winston.
- Wilson, E.D. (1971). Competitive and aggressive behaviour. In J.F. Eisenberg & W. Dillon (Eds), Man and beast, comparative social behaviour. Washington: Smithsonian inst. press.

- Wilson, E.D. (1975). Sociobiology the new synthesis. Cambridge: Harward Univ. Press.
- Wootton, R.J. (1972). The behaviour of the male three-spined stickleback in a natural situation: A quantitative description. Behaviour, 41, 232-241.
- Zayan, R.C. (1974). Le rôle de la reconnaissance individuelle dans la stabilité des relations hiérarchiques chez Xiphophorus (Pisces, poeciliidae). Behaviour, 49, 268-312.
- Zayan, R.C. (1975). Défense du territoire et reconnaissance individuelle chez Xiphophorus (Pisces: poeciliidae). Behaviour, 52, 266-312.

III. Methodological considerations.

The deprivation experiment

General discussion

In his 1961 discussion Lorenz delivers a thorough analysis of the advantages and limitations of the deprivation experiment. In this discussion he makes completely clear that if performed in the right way the deprivation experiment constitutes a crucial test of what is not learnt, i.e. the expression $R_{(\text{instinct})} = f(\text{genotype})$.

A deprivation experiment is an experimental treatment where the young animal is reared in isolation of some defined aspect of its natural environment. When it is later on exposed to this aspect the animal may either respond adequately to it or fail to do so. If it does respond, it is concluded that the response is not learned, but if it fails there may be a number of reasons:

- (1) The response may normally be dependent on learning.
- (2) The treatment may have been such that the animal has been withheld information necessary for the realization of the genetic blueprint.
- (3) The failure may be dependent on factors attributable to bad rearing, sampling, etc.

Thus the only thing that the deprivation experiment directly can demonstrate is what is not learned (Lorenz, 1961).

A number of objections have been raised against the use of the deprivation experiment as a critical test of the above expression (Lehrman, 1953, 1970; Hinde, 1966). The focus of the criticism has always been that the deprivation experiment de facto never can tell us whether certain behaviour is solely a function of the genome, since we never know which environmental influences are critical and can never be sure that we have substantially isolated the animal from all those environmental factors which may affect the development of the behaviour. It has been suggested that the deprivation experiment cannot tell us what is innate, but on the other hand if the animal fails to respond adequately we should have some

side, while others prior to the testing were given information either on shallowness or depth.

The outcome of the deprivation experiment was that the animals chose the shallow side. The cause of this choice could then be: innate capacity to perceive depth + innate preference for the shallow side. However, it could also be that the animals, when placed on the bridge running along the edge of the cliff prior to the choice exposed themselves to the depth cues and thereby quickly learned how to discriminate between different grades of depth. Their choice was then in accordance with what they had experienced before. Actually, several factors indicated that this also happened. In conclusion the deprivation experiment yielded no certain answer.

Now the capacity to discriminate between different grades of depth is not directly studied in a Visual Cliff situation; what is studied is the possibility of the existence of preference for shallowness or depth. Put in another way, is there such an adaptation value connected with a preference for shallowness that this preference could be considered part of an innate closed system? The answer to this question lies not in mere withholding of information but in altering information. Thus we put the organism under pressure of a specified milieu and study the interplay between organism and milieu in the developmental process.

In the experiment this was done by exposing some ducks to a deep side in a Visual Cliff, while others were exposed to a shallow side. Age and time of exposure varied. The outcome, that some eider chicks when having been exposed to a deep side in the choice situation also preferred the deep side, suggested that the preference for shallowness could not be considered part of an innate closed system. Put in another way if the genome contained a preference for shallowness, which the deprivation experiment suggested,

this preference could be changed under pressure from the milieu.

The developmental process was not fixed, some kind of learning should be in play. A careful analysis (also based on field data) made it possible to ascribe this process to the concept of imprinting (Nyström & Hansson, 1973).

Final conclusions

In conclusion the deprivation experiment offers information about the outcome of a developmental process. Thus it could not be considered a suitable tool for the study of development per se. It implies however an indication of the stability of a certain behaviour, thus indirectly its tolerance of environmental changes. In this way the deprivation experiment should still be considered a suitable tool - in studying adaptation.

R e f e r e n c e s

- Hansson, S.B. (1970). Visual depth discrimination in young eiders (*Somateria mollissima* L.). Psychol. Res. Bull., Lund Univ., 10. No. 13.
- Hinde, R.A. (1966). Animal behaviour: A synthesis of ethology and comparative psychology. London: McGraw-Hill.
- Klopfer, P.H. (1969). Instincts and chromosomes: What is an "innate" act? Amer. Naturalist, 103, 556-560.
- Lehrman, D.S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. Quart. Rev. Biol., 28, 337-363.
- Lehrman, D.S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L.R. Aronson, E. Tobach, D.S. Lehrman & J.S. Rosenblatt (Eds), Development and evolution of behavior: Essays in memory of T.C. Schneirla. San Francisco: Freeman.
- Lorenz, K. (1965). Evolution and modification of behavior. Chicago: Univ. Chicago Press (German version 1961).
- Nyström, M. & Hansson, S.B. (1973). Interaction between early experience and depth avoidance in young eider ducks (*Somateria mollissima* L.). Behaviour, 48, 303-314.

The model experiment

General discussion.

As early as 1921 v. Uexküll demonstrated that an animal can perceive only a limited part of its environment with its sense organs. Some of the perceived stimulus characteristics in the animal's environment were further demonstrated to be active only in eliciting certain behaviour; in other contexts they were of little importance. These must depend on mechanisms which are more selective than the general sensory/perceptual cues and have some degree of response specificity (Hinde, 1966).

The means by which this selection is achieved was termed *Angeborene Auslösende Schema* by Lorenz (1935) and later *Innate Releasing Mechanisms* by Tinbergen (1948). The stimulus characteristics were in the same way termed *Angeborene Auslöser* and *Sign Stimuli* respectively.

It was proposed that each *Innate Releasing Mechanism* depended on a few simple *Sign Stimuli*; that different *Sign S* added their effects to a releasing mechanism and that configurative properties among the different *Sign S* and their surroundings were important, likewise that the internal motivational state determined the threshold and intensity of the resulting action (e.g. Tinbergen, 1948, 1951).

As already mentioned the concept of *IRM* has been criticized on many grounds. In the context of stimulus filtering Hinde (1966) points at two aspects of particular interest:

(1) The term *IRM* was often used with the implication that the mechanism is specific to a particular response, although the evidence for its existence solely relies on the study of that response. In fact it has been clear that some effective stimulus characteristics are not specific to particular responses but common to many (Marler, 1961). On the other hand there is certainly no such thing as completely unspecific responsiveness. The usual situation seems to be

neither complete unspecificity nor extreme specificity but something between these according to what we assume to be the dictates of survival value and reproductive advantage (Marler & Hamilton, 1966).

(2) A second criticism of the IRM concept is that comparable selectivity from the total stimulation which impinges on the organism may depend on, or be influenced by learning: the label "innate" thus being misleading. Already the distinction between directing and releasing Sign S (Tinbergen, 1951) indicates a concept of learning (conditioning). In fact it has in many cases been possible to show that previous events ensure specific responsiveness (Marler & Hamilton, 1966).

The concept of Sign Stimulus and Innate Releasing Mechanism had its heuristic value in generating numerous studies of stimulus structures selectively connected to a particular response (Hinde & Bateson, 1976). In the last decades interest has however shifted and emphasis seems now to be on more general principles of animal perception (c.f. Andrew, 1976 on attention; Thorpe & Hall-Craggs, 1976 on gestalt principles).

The model experiment implies a successive presentation of different models to a large number of individuals and determining statistically which models produced the strongest responses. The models should differ only in one factor the influence of which is to be studied. The experimenter should be aware of the drive conditions of the animals so as to present the models when the animals are under medium drive; a drive level which is too high could induce an equal number of responses to all models, while on the other hand a drive level which is too low could lead to no responding at all. Further relational properties within the stimulus field are to be considered (Tinbergen, 1951).

It is evident that the stimulus situation is difficult to define. On one hand the organism may respond to both first- and higher-order variables, gradients of physical variables and rates of change of variables. On the other hand the character of the stimulus situation may only be an artificial abstraction of the experimenter (Hinde, 1966; Lehrman, 1953). Any attempt to isolate single physical aspects in the stimulus situation can only be a first step (a more elaborated working rationale including laboratory tests, field tests and physiological tests, has recently been suggested by Brown, 1975). In fact it has been proposed that in experiments dealing with complex visual configurations it is remarkable that simple models succeed at all in eliciting responses; in any case the response levels attained are seldom complete in comparison with the natural behaviour (Marler & Hamilton, 1966).

Hinde (1966) has remarked that the model experiment could show that some aspects of the total situation are of more importance than others, but that these experiments do not offer the tools for proving that an aspect is of no importance.

Thus being a product of a theoretical model which is too simple (the key and lock analogy) the method of isolating single physical characteristics does not seem to be an adequate way of handling the problem of selective responsiveness. Consequently it is not hard to find conflicting results obtained by model experiments. For example the findings from the famous experiments by Tinbergen and Perdeck (1950) on the pecking behaviour in young herring gulls could not be replicated by e.g. Hailman (1967) and Nyström (1969); likewise the findings from the experiments on fear of hawk shape in some young birds (Tinbergen, 1948) have been questioned by e.g. Schaller and Emlen (1962). Concerning sticklebacks, at least two later experiments have been unable to confirm the classical notation (Tinbergen,

1948) of the red colour underneath as the most potential releaser of aggression in the reproductive male (Muckensturm, 1968; Peeke, Wyers & Herz, 1969).

In a discussion of the results obtained by model experiments concerning precisely the aggression of the male three-spined sticklebacks Wootton (1976) raises the question of whether the males are really treating the model as a conspecific and potential rival. An important finding speaking against this is that after habituation towards models the introduction of a live male again evokes aggression (Peeke, 1969; also found by e.g. Martin & Melvin, 1964, in connection with the controversy about the interpretation of the hawk experiments as mentioned earlier). It could be argued that these findings are in line with what could be expected from the general conception of "heterogeneous stimulus summation" (Seitz, 1940; Tinbergen, 1948) - it may however also be that the artificiality and poverty of the models makes a difference in responsivity not merely in the matter of quantity but also of quality. Such a qualitative difference was reported in this connection by Wootton in his article on methodology in experiments with sticklebacks (1971). He found that sticklebacks make their approaches to models with both dorsal and pelvic spines erect, while they will approach live specimen with either no spine or dorsal spines alone erect. Now the motivational causes behind spine raising, and different kinds of spine raising, is unclear (see Hansson, 1978a, for a discussion) but it has been suggested that erection of at least the pelvic spines might indicate fleeing instead of aggression (v. Iersel, 1953; Symons, 1965). Thus it might be that the responses directed to the model did not reflect merely aggression but also constituted a reaction to novelty (Wootton, 1971).

On the other hand it has been found that sticklebacks show changes in level of aggression during different phases of

the reproductive cycle (Wootton, 1970). In his 1971 study it was possible for Wootton to show that the male level of aggression varied in approximately the same manner towards red (male) models, while the behaviour against a silver model varied in the same way as aggression against female conspecifics. However, with reference to the qualitative differences mentioned above it seems questionable if this could be taken as a crucial proof that male sticklebacks do treat models as live specimen. Further the males could still treat the red models as novel objects - the change in aggression or tendency to flee could then be the result of general changes in motivation, while on the other hand the silver model (as more resembling a living specimen?) could be treated as a live female conspecific.

Own contributions - discussion and summary

The model experiments on the stimulus conditions evoking aggressive display in the male three-spined sticklebacks reported in this thesis (Hansson, et al., 1971; Hansson, 1973) are closely connected with the discussion of the relevance of the "key and lock-analogy". Starting with the observation that sticklebacks direct their charges against certain parts of the body of the antagonist, and especially the eyes (van Iersel, 1953; Hall, 1956 cited in Wootton, 1976) it was proposed that in comparison with "red underneath" the gestalt "red underneath and blue eyes" constituted a more potential releaser than earlier had been suggested (Tinbergen, 1953). The results confirming this hypothesis were interpreted in two ways:

- (1) The differences obtained were in line with what could be expected when considering the law of heterogeneous stimulus summation mentioned earlier. This was a conservative explanation and it seemed to be of little heuristic value.
- (2) It was further proposed that the differences obtained might depend on the gestalt "red underneath and blue eyes" yielding a greater attention value than just "red underneath".

The latter hypothesis led to experiments where differences in attention value were operationally defined as differences in achromatic brightness contrast. In these experiments fish in the early phase of the reproductive cycle were used, since the male have not yet started to show reproductive behaviour against females then (otherwise the models could be treated as more or less adequate female conspecifics).

With the exception of the responses directed towards the silver model the suggestion that males in general react with greater intensity to models with higher attention value than to models with lower attention value was confirmed. Thus if a capacity to identify conspecifics is taken for granted (as has been demonstrated by Kennlyside, 1955) a reasonable interpretation could be that the male colouration while still serving as a releaser for female reproductive behaviour has as its primary function to orient the territory defending males. Secondly it may become a target for reproductive aggression as a consequence of experience during the early reproductive phase.

The different reactions to the silver model could be a consequence of its being confused with a female conspecific. It could also be a consequence of its being the most familiar (less novel) object among more unfamiliar objects. None of these explanations either invalidates the empirical findings or speaks against a suggestion that the models were treated as real fish. The discrepancy can on the other hand not be considered as proving that all models or in fact any model were treated as real fish. The silver model could have been confused, the other not; further a physical scale often does not correspond with a subjective scale. Thus the results highlight the ambiguity of findings based on model experiments.

R e f e r e n c e s

- Andrew, R.J. (1976). Attentional processes and animal behaviour. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge: Cambridge Univ. Press.
- Brown, J.L. (1975). The evolution of behavior. New York: W.W. Norton.
- Hailmann, J.P. (1967). The ontogeny of an instinct: The pecking response in chicks of the Laughing Gull (*Larus atricilla* L.) and related species. Behaviour, suppl., 15, 1-159.
- Hansson, S.B., Holmqvist, B. & Strömberg, I.B. (1971). Colour structures and extinction of aggressive display in the male three-spined stickleback (*Gasterosteus aculeatus* L.). Psychol. Res. Bull., Lund Univ., 11, no. 2.
- Hansson, S.B. (1973). The influence of stimulus contrast on the aggressive display of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Mimeo, Lund University.
- Hansson, S.B. (1978). Notes of the ethological method of observation. I. Selection of behavioural units. Mimeo, Lund University.
- Hinde, R.A. (1966). Animal behaviour: A synthesis of ethology and comparative psychology. London: McGraw-Hill. 2nd ed. 1970.
- Hinde, R.A. & Bateson, P.P.G. (Eds). (1976). Growing points in ethology. Cambridge: Cambridge Univ. Press.
- van Iersel, J.J.A. (1953). An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour, suppl., 3, 1-159.
- Keenleyside, M.H.A. (1955). Some aspects of the schooling behaviour of fish. Behaviour, 8, 183-248.
- Lehrman, D.S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. Quart. Rev. Biol., 28, 337-363.
- Lorenz, K. (1935). Die Kumpan in der Umwelt des Vögels. J. Ornithol., 83, 137-213, 289-413.
- Marler, P. (1961). The filtering of external stimuli during instinctive behaviour. In W.H. Thorpe & D.L. Zangwill (Eds), Current problems in animal behaviour. Cambridge: Cambridge Univ. Press.

- Marler, P. & Hamilton, W.J. (1966). Mechanisms of animal behavior. New York: J. Wiley.
- Martin, R.G. & Melvin, K.B. (1964). Fear responses of bob-white quail (*Colinus virginianus*) to a model and live red-tailed hawk (*Buteo jamaicensis*). Psychol. Forschung, 27, 323-336.
- Muckensturm, B. (1968). La réaction des Epinoches aux leurres ne provient pas d'une confusion avec un congeuere. CR.Acad. Sc. Paris (D), 226, 2114-2116.
- Nyström, M. (1969). The development of stimulus preferences in the pecking behaviour of young Herring Gulls (*Larus argentatus*). III. A replica of Tinbergen's and Perdeck's classical investigation with an alternative interpretation. Psychol. Res. Bull., Lund Univ., 9, No. 10.
- Peeke, H.V.S. (1969). Habituation of conspecific aggression in the three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour, 15, 137-156.
- Peeke, H.V.S., Wyers, E.J. & Herz, M.J. (1969). Waning of the aggressive response to male models in the three-spined stickleback (*Gasterosteus aculeatus* L.). Anim. Behav., 17, 224-228.
- Schaller, G.B. & Emlen, J.T. (1962). The ontogeny of avoidance behaviour in some precocial birds. Anim. Behav., 10, 370-381.
- Seitz, A. (1940). Die Paarbildungen bei einigen Cichliden I. Zeitschr. Tierpsychol., 4, 40-84.
- Symons, P.E.K. (1965). Analysis of spine-raising in the male three-spined stickleback. Behaviour, 26, 1-74.
- Thorpe, W.H. & Hall-Craggs, J. (1976). Sound production and perception in birds as related to the general principles of pattern perception. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge. Cambridge Univ. Press.
- Tinbergen, N. (1948). Social releasers and the experimental method required for their study. Wilson Bull., 60, 6-51.
- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press.

- Tinbergen, N. (1953). Social behaviour in animals. London: Methuen.
- Tinbergen, N. & Perdeck, A.C. (1950). On the stimulus situation releasing the begging response in the newly hatched Herring Gull chick (*Larus argentatus*, Pont.). Behaviour, 3, 1-39.
- Wootton, R.J. (1970). Aggression in the early phases of the reproductive cycle of the male three-spined stickleback (*Gasterosteus aculeatus*). Anim. Behav., 18, 740-746.
- Wootton, R.J. (1971). Measures of the aggression of parental male three-spined sticklebacks. Behaviour, 40, 228-262.
- Wootton, R.J. (1976). The biology of the sticklebacks. London: Academic Press.

M e t h o d s o f o b s e r v a t i o n

General discussion.

From the beginning it has been a distinguishing mark of ethology to start investigations with a complete inventory of the behavioural patterns of a species, e.g. to make an ethogram. Such a catalogue should be made before selecting special problems for study (Tinbergen, 1951). The reasons for making ethograms are twofold: (1) The ethogram may have a value per se since it more or less directly constitutes a tool for taxonomic and evolutionary studies. (2) Above all it may constitute a baseline against which the effects of particular stimulation can be studied. The manner in which we interpret the effects of a stimulus may be quite different depending upon whether or not we are fully acquainted with the behaviour of the unstimulated organism (Hutt & Hutt, 1970).

The description of behaviour.

The normal strategy is as follows: The first phase in the description has a broad inductive basis as free from interpretations as possible and aims at unfolding the way in which motor patterns are organized. At this stage behaviour is usually described in terms of patterns of activity in specific muscles or in terms of changes in grosser parts of the body. The descriptions are intended to be made in objective terms thus every effort is ideally made to record just how the spatial pattern is constructed; sound and odours are recorded and, most essentially, the temporal organisation of these elements is recorded (Marler & Hamilton, 1966).

The approach could then proceed to still finer analyses of specific action patterns or to broader temporal groupings of patterns and sequences in which they appear. At this stage it could further be suitable to consider environmental changes and to describe behaviour with reference to these. Further the study may lead to manipulations of the inner or outer milieu (Altmann, 1962; Schneirla, 1950).

This general strategy will certainly yield on overwhelming mass of data (selection of data has been discussed elsewhere Hansson, 1978 a). In the case of making an ethogram the rationale is usually then to select descriptive categories which are large enough to fit an extensive study in a particular manner and yet sufficiently restricted to distinguish between different forms of behaviour (Marler & Hamilton, op. cit.).

Hinde (1966) points out that in certain instances a description based on consequences would be preferable to a description based on changes in body parts. Obviously this is the case when dealing with search behaviour, but further also in instances where the complexity of data is high and where data cannot lend themselves to division into classes with objective validity. According to Hinde descriptions by consequences sometimes are the only suitable method, behaviour of members in groups could constitute a case of this (Simpson, 1973 a).

However, description in terms of consequences should not be confused with descriptions in terms of function. When the ethologist lumps together action patterns in the term "approach" he refers to the proximate consequences, not the ultimate consequences. Terms like "aggression, escape" etc. include interpretations and should be abandoned in connection with the initial description (Altmann, 1962). The risk for descriptions in functional terms would however never be actualized if the concept of function was only used in its stronger sense (as suggested by Hinde, 1975) that is: biological advantageous consequences through which natural selection acts.

Classification of behaviour patterns.

Interpretations move in when the ethologist is classifying behaviour in broader categories. Traditionally there are three approaches in classifying (Hinde, 1966): (1) causal

classification (2) functional classification and (3) historical classification (the last category is most often applied to evolutionary studies).

Earlier causal classifications were dependent on the energy model of motivation assuming specific unitary drives. Behaviour is then classified according to which drive it expresses. The main disadvantage with such an approach is the fact that causal and functional classifications could easily be confused (Hinde, 1966). With an increasing dissatisfaction with the energy models as such, new instruments were looked for; the most important among these is the sequence analysis and its modifications (Slater, 1973).

The major assumption behind the use of sequence analysis is that some behaviour patterns occur more frequently in temporal juxtaposition than others. Thus on the basis of a few elements we could be able to predict what the outcome of a particular sequence of behaviour could be (Hutt & Hutt, 1970).

Most sequence analysis of behaviour is concerned with establishing and identifying first order dependencies, that is a matrix of observed transition frequencies is compared with what would be expected if all acts were independent of each other. This treatment could be followed either by an evaluation of the potential influence of higher order dependencies, or by an analysis to detect those transitions which are significantly more common than their expected values (Slater, 1973). Cluster analysis as well as factor analysis may be applied (see e.g. the discussion by Dawkins, 1976, Nyström, 1977, and Wiepkema, 1961).

It is generally considered by ethologists that the occurrence of two behaviour patterns close together in time indicates that they have some causal factor in common. It should however be pointed out that sequence analysis only gives an

indication of which relationship needs to be explained. The description of behaviour provides hypotheses but not explanations, behaviour patterns could be associated by exclusion or because of the particular characteristics of the experimental situation (Slater, 1973).

Since ethology rests heavily on the theory of evolution the concept of function is central (Tinbergen, 1963). Functional classification and functional explanations have however been considered risky (Hinde, 1975), on the one hand because they are easily confused with those of causation, and on the other hand because they involve an element of prediction (Simpson, 1973 a). Within the new socio-biology (Wilson, 1975; Barash, 1977) the concept of function gets a somewhat different content since it is defined with reference to the individual as a part of a group. Explanations with reference to function and evolution are central in socio-biology, therefore functional classification (in the sense of socio-biology) may also become central in the future.

Concerning historical classifications, patterns of behaviour believed to have a common historical origin are grouped together; the basic criterion for grouping is similarities in the pattern of muscular contractions. The technique is most frequently used in the study of evolution of behaviour (Hinde, 1966).

Observations on social interaction.

Sequences of interaction between individuals differ from sequences of behaviour within the individual where the external world is presumed to be relatively unchanging, since the aim of the analysis of social sequences is to demonstrate that the behaviour of one animal is affected by that of others. This could be considered a more difficult task since there are two main problems connected with it:

- (1) The most interesting behaviour patterns are often those

which change in probability as the interactions proceeds.

(2) The behaviour of an animal in a social situation is likely to depend partly on the sequence of acts that it has already shown as well as on the behaviour of others (Slater, 1973). Obviously sequence analysis could only be a first step in a causal study of social communication.

In social ethology the central relations are those of the individuals and the natural group considered as the social environment within which they live and to which they are adapted (Crook, 1970 a). Emphasis should then be not on the individual and the organisation of behaviour patterns within the individual but on the organisation of the individual's behaviour towards the group as a whole and towards individuals within the group (Simpson, 1973 b). Thus social ethologists use correlational methods to look for relations among the frequencies of different behaviour patterns by an individual towards its several partners. It has been argued (Simpson, 1973 a) that it is not altogether feasible to distinguish approaches concerned primarily with causation from those concerned with function in social ethology. In social interactions it is difficult to recognize causes and effects with each distinguishable social action when the actions are taken one by one. However, it is proposed that patterns can be discerned when they are considered in groups (Altmann, 1965; Simpson, 1973 a).

Own contributions - discussion and summary.

Although not field studies, the observational studies reported in this thesis fall well within the frame of the social ethological approach (Hansson, 1978 a and b). The prime goal of these studies was to further develop the evaluation of sampling methods potentially applicable to social ethology already begun by Altmann (1974). The secondary aim was to study the interplay between social organization and social dynamics over a certain passage of time and with defined groups of cichlids (*Pterophyllum scalare*)

generally in the way suggested by Simpson (1973 a and b).

Choice of behavioural units.

The first study in this section of the thesis (Hansson, 1978 a) centers around the question of adequate selection of behavioural units. It has been stressed many times that an optimistic view of the possibility of making observations unselective and with an empty mind (Carthy, 1966) is an un-reachable task (e.g. Schneirla, 1950; Altmann, 1962; Bateson, 1968), and that, on the contrary, criteria for how intentional selection should be made must initially be carefully considered (Altmann, 1962; Marler & Hamilton, 1966). In the first section of the report the influence of the personal equation is discussed (c.f. Schneirla, 1950) and the importance of a full consideration of this phenomenon is stressed. As Schneirla (op. cit.) has pointed out there exists in this respect no qualitative difference between observation and experimentation, although the possibilities for control are less in observation (c.f. also Rosentahl, 1966 concerning experimenter effects).

In this section we also discuss criteria for classification of behavioural units into categories (categories either delimiting the study itself or functioning as shorthand descriptions for certain motor patterns within the study). With reference to the discussion of the causation of spine-raising in sticklebacks (Symons, 1965) it is suggested that behaviour patterns not objectively assignable to any category (c.f. Slater, 1973) should only be considered in relation to the context (Simpson, 1973 a).

Further in this respect the concept of hierarchy is concerned as another aspect of the significance of a proper unit selection for the validity of a problem centered observational study. It has been questioned whether in fact hierarchy could be considered as a unitary concept (Gartlan, 1968; Crook, 1970 b) and the importance of cross correlating

qualitatively different behaviour patterns has been stressed (e.g. Richards, 1974). In accordance with these suggestions individual frequencies of agonistic responses are compared with individual degrees of locomotor activity. The inverse relation which was found between these measures contributes to the consideration of the hierarchy as a complex concept.

In relation to the above considerations it is evident that behavioural units could be measured in two ways; they could either be considered as instantaneous events (yielding frequencies) or they could be considered as events with a certain time-range (yielding durations) (Altmann, 1974). Since this is also evident for units within the same behavioural category the validity of a certain class of behaviour as an indicator of a hierarchy could also be considered for relations between measures within the same category (c.f. Simpson, 1973 b). In contrast to the findings from the Simpson study (which was made with chimpanzees) these two measures were found to co-vary although individual differences prevented the correspondence from being unanimous. A significant finding from this part of the study is that measures of durations with low responsive fish tended to decrease with time while measures of durations with high responsive fish tended to increase. Since this trend was not to be found when comparing frequencies, durations may be a more sensitive measure of a process commonly found in groups with high population density (Archer, 1970 concerning rodents).

The last section in this report centers around the individual as performing the double role of producer and receiver in a social interaction (Altmann, 1974). The result of the analysis points towards an interactive relationship between these two aspects of the individual's social behaviour. Thus no one of these measures alone could yield a complete and valid description of the hierarchy.

Further since the same interactive patterns were found in two groups the result may indicate that a conception of a hierarchy in terms of roles (Rowell, 1966; Bernstein & Sharpe, 1966; Gartlan, 1968 all concerning primates) as distinct social positions within a group structure independent of the particular members of the group (Crook, 1970 b) may also be justified with regard to the species studied here. However, since the fundamental work on these hypotheses (the role concept) has been done on primates, we prefer the term individual styles of adaptation, we indicate thereby that individual fish behave qualitatively differently within each group and that this may have a functional value (as is discussed in the later report, Hansson, 1978 b).

The last finding in this section is that a newly composed group is more susceptible to changes in dominance relations than an already settled group. This finding is in line with the general conception of social dominance as a product of social learning (Ginsburg & Allee, 1942 concerning rodents; Rowell, 1966 concerning primates).

Focal animal sampling.

The second report in this section of the thesis (Hansson, 1978 b) centers around the problem of choosing adequate sampling methods (discussed earlier by Altmann, 1974). Basic in these studies is the conviction that the aquarium constitutes a valuable miniature situation for the development and testing of sampling methods for later use in the field. The aim of all the techniques discussed is to facilitate analyses of structure and dynamics of social interaction within groups of animals.

Attention is focused upon the method of focal animal sampling. It is recognized that although this method constitutes an efficient tool when aiming at making descriptions, it offers fewer opportunities for applying sequence analysis to data. Thus the empirical part of the report is mainly descriptive

in character; causal interpretations are used restrictively.

Data were mainly treated in two ways: (1) Analyses of frequencies without consideration of direction of choices. (2) Analyses of frequencies with consideration of direction of choices. Thus the analysis was made in two steps of ascending refinement. The strategy behind this procedure was to find out if a simple quantitative analysis would yield as valid a description of a hierarchy as would a more complex qualitative analysis, or if a qualitative analysis would necessitate any decisive additions or changes in the interpretation of data. The result indicates that these two approaches in fact complement each other, thus confirming what has been said earlier about the complex nature of a hierarchy.

The results were discussed with reference to three major themes (of which the first is only supplementary to the content and purpose of the study): (1) External validity. (2) Internal validity. (3) Reliability. Concerning external validity it was concluded that analyses on the switch from territoriality to dominance with higher population density (Wilson, 1975) may have a heuristic value in the study of the evolution of pair-building behaviour.

Basic to the discussion of internal validity is the truism that there could be no hierarchy without any consistency of individual behaviour in relation to other members of the group. Firstly, the results did not indicate the existence of any absolute linear dominance hierarchy; the social system revealed here could best be described in terms of relative, branching hierarchies, and even this is less certain when considering the females. Thus it is again confirmed that the concept of hierarchy is complex, and that it might be justified to replace hierarchy with terms such as "roles" (Gartlan, 1968) or styles of adaptation (Hansson, 1978 a). Secondly, in spite of this, data did

show statistically sufficient consistency. Thus whatever the social system might be called it appears to be relatively stable.

Further, the above discussion indicates that it is possible within the range of the focal method to establish criteria for internal validity and to make measurements in relation to these criteria. The absence of absolute consistency could be explained with reference to the limited time range of the studies and with reference to a hierarchy as a social learning process (as has been discussed above) rather than a stationary phenomenon (Crook, 1970 b).

No index of observer reliability is calculated, however the demonstration of such an index does not seem to be central for the purpose of the investigation (c.f. Costello, 1973). In fact the conditions underlying much field work with at least higher mammals are such that only one observer at a time could be involved. Secondly since both acts produced and received and the direction of these were recorded it became possible to check measurements obtained within the focal periods of each specific individual against measurements obtained outside these periods. Agreement was found to be high. Thus there is an inherent capacity for judging reliability within the focal method.

Although the observational studies reported in this thesis well illuminate the width of possibilities inherent in the observational approach to animal behaviour it should nevertheless be brought out clearly that no deeper understanding of any phenomena will ever be reached only by performing descriptive studies. The descriptive observational approach should be followed by a causal one and this by experimental tests (Schneirla, 1950). The description constitutes only a preparatory stage.

Observations on humans.

Recently the observational approach of ethology has been transferred from infrahuman animals to man (see e.g. Hutt & Hutt, 1970; Blurton Jones, 1972). The ethologists working with man have in common with those working with different infrahuman species that they aim towards making an ethogram of the species (Tinbergen, 1972). The techniques behind these studies are the same as those used with animals. It is our impression that these studies may prove most fruitful when concentrating on the behaviour of new-born children where the temporal ordering of motor patterns can be more or less directly related to physiological events (e.g. Nyström, 1975). Dealing with the behaviour of older children and with that of adults the value of the ethological approach may be diminished by uncontrollable influence from different social settings, the differentiating process of socialization and the individual's past history (see however also the critical article by Cooper et al., 1974).

R e f e r e n c e s

- Altmann, S.A. (1962). A field study of the socio-biology of rhesus monkeys, *Macaca mulatta*. Ann. N.Y. Sciences, 102, 338-435.
- Altmann, S.A. (1965). Sociobiology of rhesus monkeys. II. Stochastics of social communication. J. Theoretic. Biol., 8, 490-522.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49, 227-267.
- Archer, J. (1970). Effects of population density on behaviour in rodents. In J.H. Crook (Ed.), Social behaviour in birds and mammals. London: Academic Press.
- Barash, D.P. (1977). Sociobiology and behavior. New York: Elsevier.
- Bateson, P.P.G. (1968). Ethological methods of observing behavior. In L. Weiskrantz (Ed.), Analysis of behavioral change. New York: Harper & Row.
- Bernstein, I.S. & Sharpe, L.G. (1966). Social roles in a rhesus monkey group. Behaviour, 26, 91-104.

- Blurton Jones, N. (Ed.). (1972). Ethological studies of child behaviour. Cambridge: Cambridge Univ. Press.
- Carthy, J.D. (1966). The study of behaviour. London: Arnold.
- Cooper, E.S., Costello, A.J., Douglas, J.W.B., Ingleby, J.D. & Turner, R.K. (1974). Direct observation? Bull, Br. psychol. Soc., 27, 3-7.
- Costello, A.J. (1973). The reliability of direct observations. Bull. Br. psychol. Soc., 26, 105-108.
- Crook, J.H. (1970 a). Social organisation and environment: Aspects of contemporary social ethology. Anim. Behav., 18, 197-209.
- Crook, J.H. (1970 b). The socio-ecology of primates. In J.H. Crook (Ed.), Social behaviour in birds and mammals. London: Academic Press.
- Dawkins, R. (1976). Hierarchical organisation: A candidate principle for ethology. In P.P.G. Bateson & R.A. Hinde (Eds), Growing points in ethology. Cambridge: Cambridge Univ. Press.
- Gartlan, J.S. (1968). Structure and function in primate society. Folia Primat., 8, 89-120.
- Ginsburg, B. & Allee, W.C. (1942). Some effects of conditioning on social dominance and subordination in inbred strains of mice. Physiol. Zool., 15, 485-506.
- Hansson, S.B. (1978 a). Notes on the ethological method of observation. I. Selection of behavioural units. Mimeo. Lund University, Lund.
- Hansson, S.B. (1978 b). Notes on the ethological method of observation. II. Focal animal sampling. Mimeo. Lund University, Lund.
- Hinde, R.A. (1966). Animal behaviour: A synthesis of ethology and comparative psychology. London: McGraw-Hill. 2nd ed. 1970.
- Hinde, R.A. (1975). The concept of function. In G. Baerends, C. Beer & A. Manning (Eds), Function and evolution in behaviour. Oxford: Clarendon Press.
- Hutt, S.J. & Hutt, C. (1970). Direct observation and measurement in behavior. Springfield: C.C. Thomas.

- Marler, P. & Hamilton, W.J. (1966). Mechanisms of animal behavior. New York: Wiley.
- Nyström, M. (1975). Neonatal facial-postural patterning during sleep. II. Activity and states. Psychol. Res. Bull., Lund Univ., 15, No. 1.
- Nyström, M. (1977). Neonatal facial-postural patterning during sleep. V. Ethological models and temporal organisation, Psychol. Res. Bull., Lund Univ., 17, no. 9.
- Richards, S.M. (1974). The concept of dominance and methods of assessment. Anim. Behav., 22, 914-930.
- Rosenthal, R. (1966). Experimenter effects in behavioral research. New York: Appleton Cent. Crofts.
- Rowell, T.E. (1966). Hierarchy in the organization of a captive baboon group. Anim. Behav., 14, 420-443.
- Schneirla, T.C. (1950). The relationship between observation and experimentation in the field study of behavior. Ann. N.Y. Acad. Sciences, 51, 1022-1044.
- Simpson, M.J.A. (1973 a). Social displays and the recognition of individuals. In P.P.G. Bateson & P.H. Klopfer (Eds), Perspectives in ethology. New York: Plenum Press.
- Simpson, M.J.A. (1973 b). The social grooming of male chimpanzees. In R.P. Michael & J.H. Crook (Eds), Comparative ecology and behaviour of primates. London: Academic Press.
- Slater, P.J.B. (1973). Describing sequences of behavior. In P.P.G. Bateson & P.H. Klopfer (Eds), Perspectives in ethology. New York: Plenum Press.
- Symons, P.E.K. (1965). Analysis of spine-raising in the male three-spined stickleback. Behaviour, 26, 1-74.
- Tinbergen, N. (1951). The study of instinct. Oxford: Oxford Univ. Press.
- Tinbergen, N. (1963). On aims and methods of ethology. Zeitschr. Tierpsychol., 20, 410-433.
- Tinbergen, N. (1972). Foreword in N. Blurton Jones (Ed.), Ethological studies of child behaviour. Cambridge: Cambridge Univ. Press.

Wiepkema, P.R. (1961). An ethological analysis of the reproductive behaviour of the bitterling (*Rhodeus amarus*, Bloch). Arch. Neerl. Zool., 14, 103-199.

Wilson, E.O. (1975). Sociobiology: The new synthesis.
Cambridge: Harvard Univ. Press.

